The Scottish Office
Agriculture and Fisheries
Department in Association with
The Spey District Salmon
Fishery Board

The Movements of Adult Atlantic Salmon (*Salmo salar* L.) in the River Spey as Determined by Radio Telemetry during 1988 and 1989

Robert Laughton

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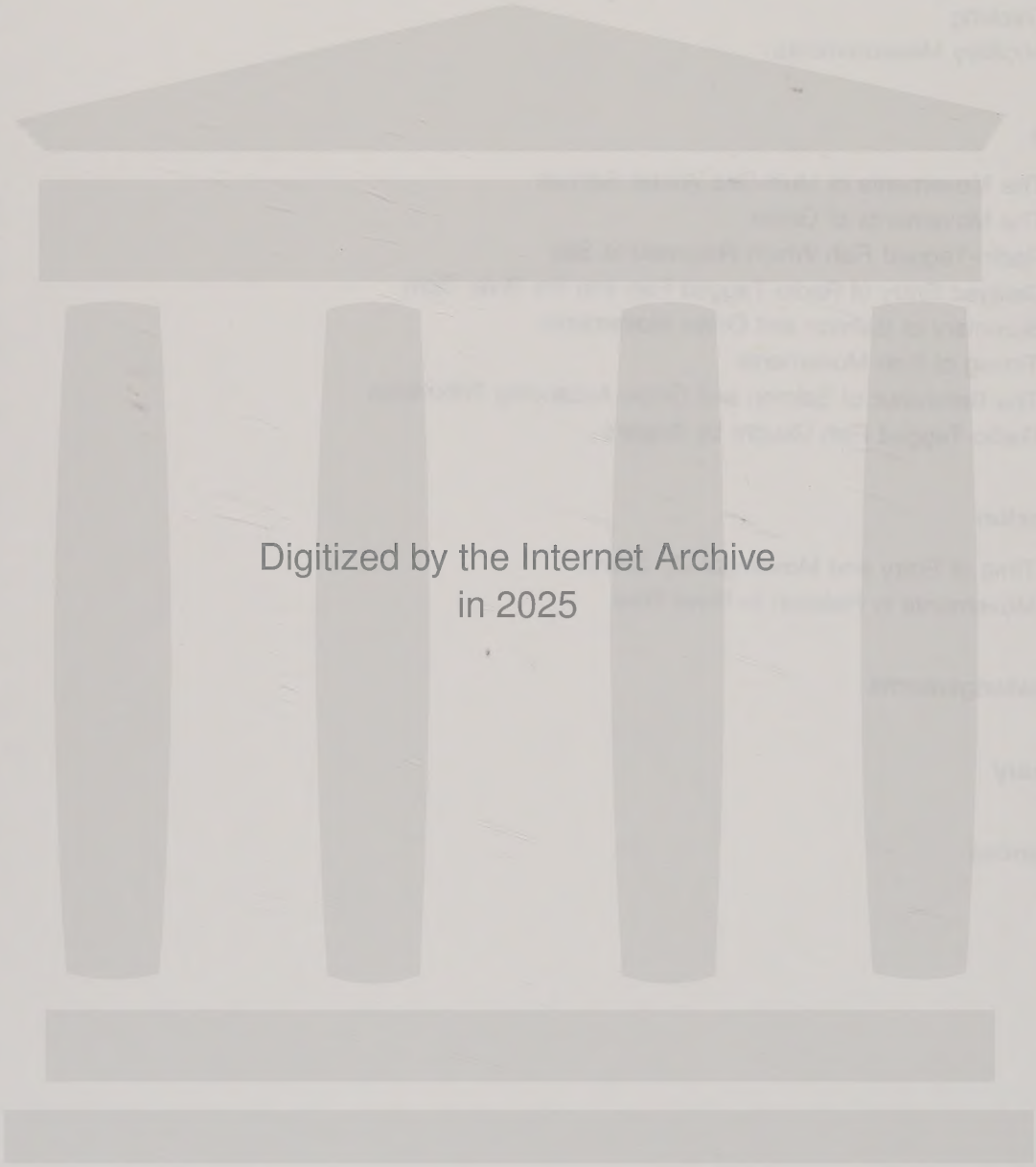

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Foreword

This is the second and final report describing a research project initiated by the Spey District Fishery Board in 1988, with the help of the Marine Laboratory of The Scottish Office Agriculture and Fisheries Department. The project forms part of a continuing research programme by the Spey Board, aimed at obtaining a greater knowledge of the requirements and behaviour of salmon in the Spey through which the management of the salmon stocks and fishery may be improved.

This specific project was set up to improve our understanding of factors affecting the spring run of salmon on the Spey, a run which is nowadays very much weaker than it once was. The behaviour of individual fish entering the Spey at different times of the year was examined by tagging them with small radio-transmitters. Over the two years of study, 69 salmon were tagged and released, and the majority of these fish were subsequently followed up stream for many months, and much detailed information has been gained on their journeys within the river.

The main finding of the study has been that spring salmon, those fish entering the river in the early part of the year after spending at least two and sometimes more winters in the sea, migrate to and spawn in the upper reaches of the Spey. Early grilse, those fish spending a single winter in the sea, re-entering the river in June, also tended to spawn in the upper reaches. Later entrants of both types spawned in the lower reaches. Therefore, a clear pattern of behaviour has emerged.

Of the 36 true spring fish examined (those entering before 1 May), 11 were recaptured by anglers, one of them in the Findhorn (having moved down stream to re-enter the sea), and the others in the Spey and its tributaries. Far fewer of the later entrants were recaptured (one out of 33). These results may indicate a greater vulnerability of spring fish to angling, which should cause us some concern perhaps.

This detailed and instructive study would not have been possible without the enthusiasm of Superintendent Jim Gray and his team of bailiffs, the willingness of the salmon netsmen who captured the fish for tagging, and the interest of the various proprietors, anglers and ghillies, who also provided help and advice. We would also like to express our gratitude to the small number of sponsors who enabled the study to take place, especially:

The Highland and Islands Development Board
The Crown Estate Commissioners
The MacRobert Trusts
The Atlantic Salmon Trust Ltd
Baxters of Speyside Ltd
Eagle Star Insurance Company Ltd
Stakis PLC
Walkers Shortbread Ltd (Aberlour)

Finally we would like to record our thanks to Robert Laughton, the author of this report, for his dedication to the study.

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The Movements of Adult Atlantic Salmon (*Salmo salar* L.) in the River Spey as Determined by Radio Telemetry During 1988 and 1989

Robert Laughton*
Marine Laboratory,Aberdeen

***Employed by The Spey District Salmon Fishery Board**

Introduction

In April 1988, the Spey District Salmon Fishery Board, in conjunction with The SOAFD Marine Laboratory, Aberdeen, began a two year study into the migrations of returning adult salmon within the River Spey. During the two years, salmon and grilse caught in the net and coble fishery near the river mouth were radio-tagged, released, and their behaviour was monitored as they progressed up stream. Investigations during the first year are reported by Laughton (1989).

Telemetry has been widely used in the study of salmon returning to their home waters. Hawkins *et al.* (1979) examined the movements of fish in coastal waters; Stasko (1975), Brawn (1982) and Phillips (1989) followed movements through estuaries; while Hawkins and Smith (1986), Webb (1989, 1990) and Webb and Hawkins (1989) observed the riverine migrations of salmon. Radio telemetry allows the movements of an adult salmon to be recorded in detail throughout the duration of its up-stream journey. These movements can then be related to variations in environmental conditions, such as flow rates, river temperature and light levels.

In recent years there has been a decline in the numbers of spring salmon, those fish which enter the river before 1 May, caught by anglers and netsmen on the Spey (Shearer, 1988). Similar trends have been reported from other east coast Scottish rivers such as the Dee (Shearer, 1985) and the Tay (Gardiner, 1971). The reasons for this decline are as yet unclear.

The behaviour of the spring salmon is poorly documented and the primary objective of this study was to examine the movements and ultimate spawning destinations of these fish. However, the study also examined the migratory behaviour of salmon and grilse entering later in the year, allowing seasonal differences in the destination of the fish to be determined.

Materials and Methods

The River Spey

The River Spey is one of the largest rivers in Scotland, having a total catchment of 2,988 km^2 (1,154 square miles) (Goody, 1988) and an average daily flow of 64 m^3 s^{-1} at Boat o'Brig, the lowest main stem gauging station (Inglis et al., 1988). In size, it is rivalled only by the Tay and the Tweed. From its source at Loch Spey in the Monadhliath Mountains it flows approximately 157 km (97 miles) to the Moray Firth. Apart from Spey

Dam, operated by British Alcan, near Laggan in the upper reaches, there are no other obstructions along the main stem.

Most of the major tributaries of the Spey, namely the Truim, Tromie, Feshie, Nethy and Dulnain, drain from the Cairngorms or the Monadhliath Mountains and enter the main stem in the higher reaches.

The exception is the River Avon (pronounced A'an), the largest of the Spey's tributaries. From its source at Loch Avon, some 700 m above sea level, on the south east side of Cairngorm, it flows approximately 55 km (34 miles) to reach the main stem of the Spey at the Junction Pool, Ballindalloch, 50 km up stream from Speymouth. The average daily flow rate is 15 m^3 s^{-1}, approximately one quarter of the mean flow for the Spey itself (Inglis *et al.*, 1988).

The river is well known for its clarity of water and is reputed to be one of the clearest in Scotland (Ashley-Cooper, 1980). The tributary is fished along much of its length for both salmon and sea trout. However, few fish are taken before May with most of the catch taken from June onwards.

In common with the Aberdeenshire Dee, the Spey is an alpine river with melting snow sustaining high flow rates into late spring and early summer. The waters of the Spey are low in nutrients (oligotrophic) and have remained fairly free from pollution despite recent increases in tourism, the whisky distilling industry and changes in land use (Lambert and Little, 1988).

The river is famous for its salmon fishing, both netting and angling, and is rivalled only by the Dee, Tay and Tweed. A comprehensive review of the main biological, economic and social features of Strathspey is given by Jenkins (1988).

Radio Tagging

The salmon used for radio tagging were obtained from the net and coble fishery operated by the Crown Estate Commissioners in the lower reaches of the River Spey (Fig. 1).

Fish for tagging were quickly removed from the sweep net and placed in a tank containing anaesthetic solution (1:10,000 MS 222, Sandoz). Salmon for tagging were taken at random from the sweep net and were not selected on the basis of size or sex. During anaesthesia each fish was inspected thoroughly and any fish showing superficial damage were rejected. After inspection, the fork length was measured, a scale sample obtained, and a yellow numbered Floy tag inserted into the dorsal musculature below the dorsal fin. Where possible the sex was also determined from external secondary sexual characteristics. A radio tag (Solomon and Storeton-West, 1983) was then gently inserted through the mouth and into the stomach by means of a perspex tube. The fish was then held in the river and allowed to recover before release.

Netting during the year was often limited to one pool, the Groyne, 1.7 km up stream from the river mouth, where regular catches were obtained. In order to avoid recapture of radio-tagged fish on subsequent sweeps, the fish were placed in a dark, sealed insulated fish transport box containing river water. They were then transported approximately 1 km up stream before release. The complete operation from capture to release took

between 5 and 10 minutes. The method proved to be successful, with the fish fully recovered from the anaesthesia just before release.

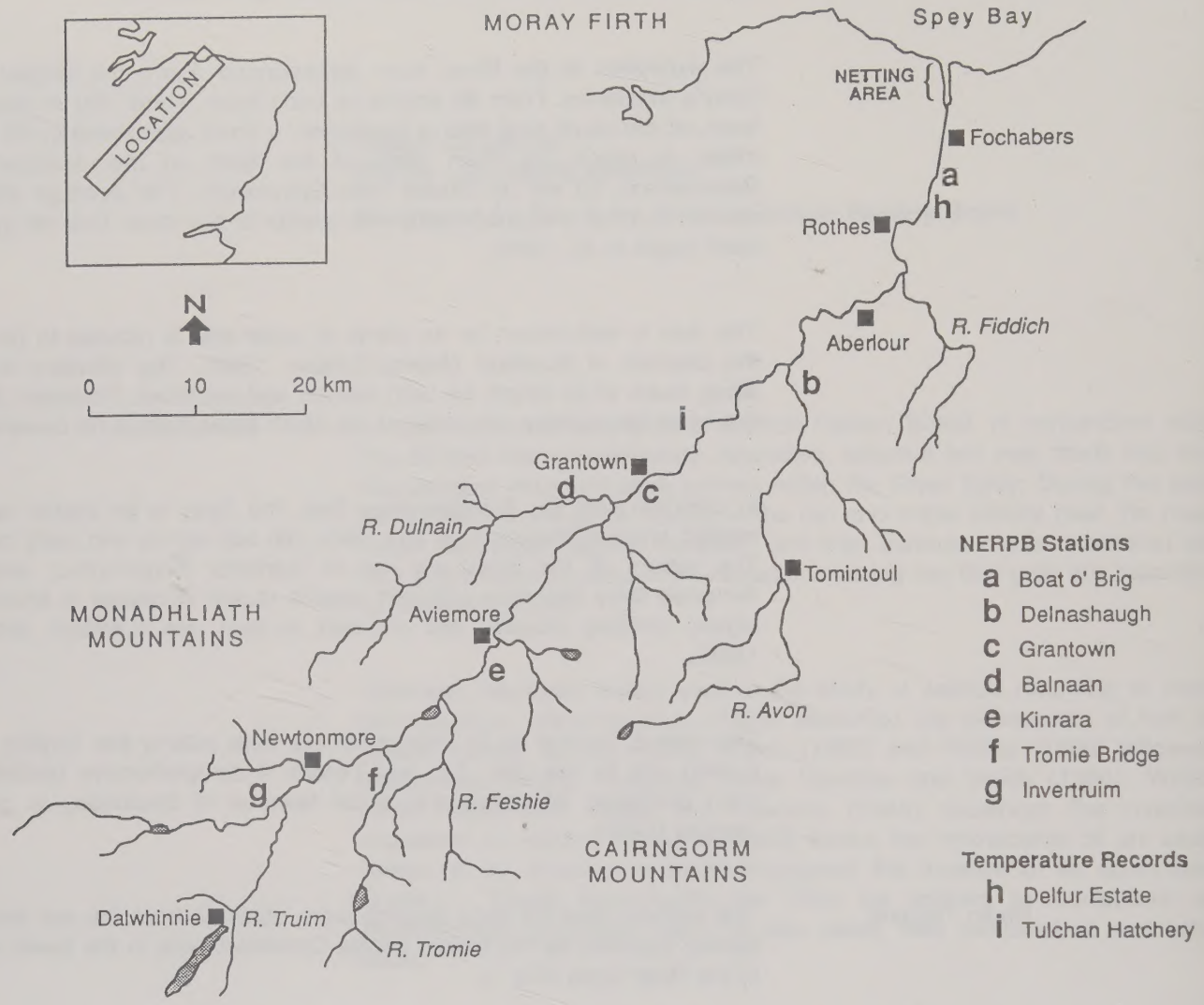


Figure 1. **Map showing the North East River Purification Board's gauging stations on the River Spey: a) Boat o'Brig; b) Delnashaugh, River Avon; c) Grantown-on-Spey; d) Balnaan, River Dulnain; e) Kinrara; f) Tromie Bridge, River Tromie; and g) Invertruim. Also shown are the positions of: h) Delfur and i) the Tulchan Hatchery, both of whom supplied river temperature data, and the location of the netting area.**

Tracking

After release fish were tracked from the river bank using a portable Yaesu FT 290R radio receiver and antenna (Solomon and Storeton-West, 1983). Automatic listening stations (ALSTNs) described by Solomon and Potter (1988) were also deployed along the length of the river. These scanned 10 different pre-set radio frequencies at five minute intervals, and recorded the presence of any fish which were within detection range, approximately 500m. As the radio-tagged salmon and grilse became widely spread throughout the length of the Spey system use was also made of a Cessna 172 light aircraft, equipped with a receiver and dipole antenna, to locate the positions of the fish. This proved to be the most effective way of tracking

fish in the more inaccessible areas such as Loch Insh, the Insh Marshes, and the higher reaches of the Avon, Feshie and Tromie tributaries.

Individual fish positions were located on an Ordnance Survey map, 1:25,000 scale, and expressed as coordinates to the nearest 50 metres. This data along with the distance moved up stream from Speymouth, the date and timing of the fix was stored on the main VAX computer at the SOAFD Marine Laboratory, Aberdeen.

Further, details of the tagging and tracking procedures for the Spey are given in Laughton (1989). Descriptions of similar techniques, applied in other Scottish rivers, are given by Hawkins and Smith (1986), Webb and Hawkins (1989) and Webb (1989, 1990).

Ancillary Measurements

Throughout the year, water flow and quality in the Spey is routinely monitored by the North East River Purification Board (NERPB). Gauging stations are operated along the main stem of the river, and many of the tributaries. Flow data was made available from several stations, including, Boat o'Brig, Grantown-on-Spey, Kinrara, and Invertruim on the main stem. Flows from the Delnashaugh station on the River Avon and Tromie Bridge on the River Tromie were also examined. Figure 1 shows the positions of these stations within the Spey catchment. Flows described in this report are the mean daily discharge (MDD) and occasionally the maximum daily discharge. The calculated rise in flow levels is shown as a percentage change from the monthly mean discharge (ie x% MMD) for that year, similar to Webb (1989, 1990).

River temperatures were supplied by the Tulchan Hatchery where they are measured daily at 0830 GMT. The Delfur Estate record river temperatures throughout the angling season and these were also made available. The respective positions of each monitoring site are shown on Figure 1.

Results

A total of 13 salmon (multi-sea-winter) and 11 grilse (one-sea-winter fish) was radio tagged and released into the River Spey during 1988. Details of each fish are given in Table I. During 1989, a further 33 salmon and 12 grilse were released and details are given in Table II. For ease of presentation the fish will be divided into spring salmon (multi-sea-winter fish entering the river before 1 May), summer salmon (those entering on or after 1 May) and grilse (one-sea-winter fish which usually enter after 1 May).

Fish tagged and released during 1988 will be referred to as Fx.88, while those released during 1989 as Fx.89. The positions occupied by fish as they progress up stream are given by the pool name followed by the distance from Speymouth in kilometres, ie Bridge pool (2 km). The timing of movements are shown in GMT.

The Movements of Multi-Sea-Winter Salmon

A total of 46 multi-sea-winter salmon was radio tagged and released during 1988 and 1989, comprising 36 spring salmon and 10 summer salmon.

The fortunes of each monthly group were quite mixed and are summarised in Table III. In total, only seven spring salmon and four summer salmon were tracked through to the spawning season. However, despite losses

from various sources, details on the early up-stream progress and the timing of the movements were collected for most fish.

TABLE I

Details of the fish tagged and released into the River Spey during 1988. Where the age of the fish is given, the first figure is the number of years spent in fresh water before migrating to the sea as a smolt; the next figure is the maiden sea age of the fish

Fish No	Release date	Date last observed	Age	Length (cm)	Sex	Remarks
1	27.04	06.10	2.2	75.0	M	Spawned River Dulnain
2	27.04	17.06	-	78.0	-	Tag failure at Tulchan
3	29.04	12.05	2.2	79.0	-	Lost Grantown
4	29.04	09.05	3.2	76.5	-	Tag failure at Brae Water
5	29.04	05.05	2.2	77.5	-	Caught River Spey
6	29.04	15.09	3.2	78.5	-	Tag failure Dulnain Mouth
7	13.05	24.05	2.2	76.5	-	Returned to sea
8	13.05	05.05	3.2	76.5	-	Tag returned*
9	13.05	24.05	-	73.0	-	Returned to sea
10	13.05	24.05	2.2	80.5	-	Returned to sea
11	20.06	19.08	-	66.0	M	Lost/left river
12	20.06	04.12	-	72.0	-	Spawned Arndilly
14	24.06	14.07	-	81.0	-	Tag failure River Avon

Radio-tagged grilse 1988

Fish No	Release date	Date last observed	Age	Length (cm)	Sex	Remarks
13	24.06	07.11	3.1	68.0	-	Spawned Newtonmore/River Calder
15	05.08	04.12	2.1	63.0	-	Spawned near Baxters, Fochabers
16	05.08	12.08	-	72.0	-	Returned to sea
17	05.08	04.12	-	70.0	-	Spawned Brae Water area
18	05.08	14.11	-	70.5	-	Spawned Orton area
19	05.08	14.09	-	67.0	-	Returned to sea
20	12.08	04.12	-	63.0	-	Spawned Rothes area
21	12.08	29.11	-	69.5	M	Spawned between Knockando and Avonmouth
22	12.08	04.12	3.1	67.0	F	Spawned Delfur area
23	12.08	04.12	3.1	63.5	-	Spawned Brae Water area
24	12.08	17.08	3.1	64.0	F	Returned to sea

*Radio tag found on the river bank near Grantown and returned - not caught by an angler as reported in Laughton (1989)

The longest continuous tracks were recorded for F16.89, F23.89 and F29.89. These salmon all progressed to the upper areas of the river, spawning in the River Tromie, the mouth of the Nethy, and below Spey Dam respectively. Figure 2 shows the complete tracks made by each of these fish together with the flow rates recorded at Boat o'Brig and Grantown

At this stage it is worth describing, in detail, the movements of these three salmon. First the behaviour of F16.89. This fish was released on 22 February at 1103 h during a falling discharge, when the MDD at Boat o'Brig was 68.4 $m^3 s^{-1}$ (70.7% of MMD). Initial up-stream progress was slow, the fish reaching Advie Bridge, Tulchan (57.5 km) by 22 March, some 30 days after release. During the ascent, a brief down-stream movement was observed on 28 February which coincided with spate conditions, the flow levels reaching 119 $m^3 s^{-1}$ at Boat o'Brig (124% MMD). Up-stream progress resumed on 1 March. After a short stop (5 days) near Advie.Bridge, further progress commenced on 27 March coinciding with flow levels of 125.1 $m^3 s^{-1}$ at Grantown (154% MMD). The fish eventually reached the Kinchurdy Pool (91.4 km), in the Kincardine Beat, on 18 April where it remained until 14 June. River flows increased on 14 June, reaching 40.17 $m^3 s^{-1}$ at Grantown (222% MMD), when a further up-stream migration to the Insh Marshes (117 km) took place. The fish remained in the Insh Marshes for over a month, eventually entering the

River Tromie. It reached Tromie Bridge (121 km) on 20 September, when the tributary was in spate with a maximum flow rate of 27.7 $m^3 s^{-1}$ (1,591% MMD). However, as tributary levels dropped reaching 1.4 $m^3 s^{-1}$ (82% MMD) on 27 September F16.89 returned to the main stem.

TABLE II

Details of the fish tagged and released into the River Spey during 1989. Where the age of the fish is given, the first figure is the number of years spent in fresh water before migrating to the sea as a smolt; the next figure is the maiden sea age of the fish

Radio-tagged salmon 1989

Fish No	Release date	Date last observed	Sex	Remarks
1	06.02	-	F	Regurgitation, tag returned 03.04
2	07.02	08.02	F	Returned to sea
3	07.02	27.02	F	Caught River Spey
4	08.02	27.09	F	Tag failure River Avon
5	08.02	08.02	M	Returned to sea
6	09.02	21.02	F	Lost Arndilly area
7	10.02	01.04	F	Lost Knockando area
8	10.02	20.04	F	Caught River Spey
9	10.02	19.07	F	Caught River Findhorn
10	20.02	10.04	F	Returned to sea
11	20.02	14.03	F	Caught River Spey
12	21.02	09.08	F	Tag failure Delfur
13	22.02	22.02	F	Returned to sea
14	22.02	11.03	F	Caught River Spey (age 3.3)
15	22.02	03.03	F	Caught River Spey
16	22.02	11.11	F	Spawned River Tromie
17	22.02	31.05	M	Caught River Spey
18	22.02	-	F	Regurgitation, tag returned 19.04
19	21.03	16.10	-	Tracked to River Avon
20	28.03	-	F	Possible tag regurgitation
21	28.03	05.09	-	Lost Delfur area
22	30.03	11.04	F	Caught River Spey (age 2.2)
23	30.03	22.11	-	Spawned River Nethy mouth
24	30.03	06.07	M ?	Tag failure
25	31.03	17.08	F	Lost Carron area
26	31.03	20.094	F	Caught River Spey
27	31.03	19.10	F	Tracked to Castle Grant
28	26.04	17.05	F	Lost River Avon
29	26.04	17.11	-	Spawned Laggan area
30	26.04	31.05	F	Caught River Spey
31	13.05	05.10	-	Spawned Rothes area
32	13.05	20.11	-	Spawned Aberlour area
34	13.05	18.10	F	Last recorded Brae Water

Radio-tagged grilse 1989

Fish No	Release date	Date last observed	Sex	Remarks
33	13.06	11.11	-	Tracked to Brae Water
35	16.06	-	-	Regurgitation, tag returned 04.09
36	16.06	16.06	-	Caught River Spey
37	16.06	18.06	-	Caught River Spey
38	16.06	17.11	-	Spawned Allt a'Chaorainn mouth area
39	16.06	14.09	-	Tag failure
40	16.06	11.11	-	Spawned Castle Grant area
41	23.06	24.11	-	Spawned River Avon
42	23.06	26.06	-	Returned to sea
43	23.06	11.11	-	Tracked to Knockando
44	23.06	17.10	-	Spawned River Avon
45	23.06	17.11	-	Spawned River Feshie

TABLE III

Summary of spring and summer multi-sea-winter salmon showing the numbers of fish lost through tag failure, possible regurgitation, return to sea, recapture by anglers and losses through unknown means

Month	No released	No rod caught	Tag failure	Possible regurgitation	Returned to sea	Unknown loss	Long-term track
February	18	7	2	2	4	2	1
March	9	2	1	1	0	1	4
April	9	2	3	0	0	2	2
May	4	0	0	0	3	1	0
June	6	0	1	0	1	0	4
Total	46	11	7	3	8	6	11

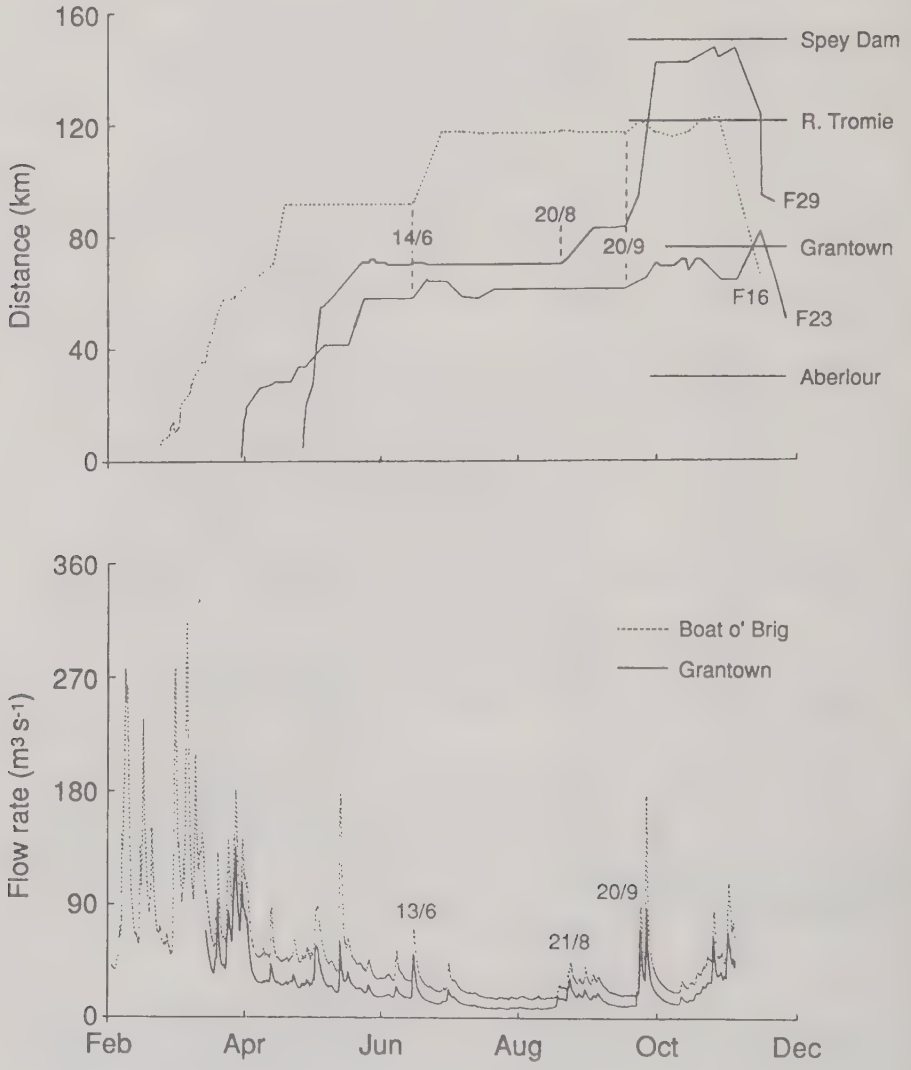


Figure 2. **The movements of spring salmon F16.89, F23.89 and F29.89. The mean daily flow conditions at Boat o'Brig and Grantown are also shown.**

F16.89 re-entered the Tromie on 17 October. No noticeable increase in tributary flow was recorded at the time of the second entry. Further progress from Tromie Bridge (121 km) to Killihuntly Farm occurred on 24 October, and it seems likely that the fish went on to spawn in the tributary. Contact was lost until 11 November when an aerial survey located the fish further down stream in the Pollwick Pool (80.9 km), Castle Grant No 3 Beat.

The tracks produced by F23.89 and F29.89 showed a similar pattern. F23.89 progressed to the Tulchan Estate, settling in the Speanoch Pool (57.8 km). During the summer it progressed further up stream to Castle Grant No 3 Beat where it remained until 8 October. Its exact spawning position was not determined but probably took place in the River Nethy area (80.9 km) where it was located on 11 November.

Of the three, F29.89 penetrated the furthest up stream. After remaining in the Congash Pool, Castle Grant (71.7 km), for most of the summer it began a further ascent of the river on 20 August when the MDD at Grantown was 26.69 $m^3 s^{-1}$ (189% MMD), reaching the old railway bridge on the Abernethy Association Water (82.51 km) on 31 August. Further progress occurred on 20 September, coinciding with an MDD of 59.55 $m^3 s^{-1}$ at Grantown (291% MMD), when the fish ascended to the Allt na Cubhaige Burn (141.2 km) near Laggan. It eventually reached and probably spawned between Laggan Bridge (142.9 km) and Spey Dam (146.5 km).

A similar pattern of migration was also shown by the spring salmon tagged and released during 1988. Thus, F1.88 released on 27 April eventually ascended the River Dulnain (97.5 km) on 6 October; further details are given in Laughton (1989).

Most of the interest in this study centred on the behaviour of spring salmon. However, to provide a basis for comparison, several summer salmon were radio tagged and released during May and June 1988 and June 1989. Details of each fish are given in Tables I and II.

Of the May fish, F7.88, F9.88 and F10.88 ascended the river but eventually returned to sea. Fish F8.88 was tracked to the Polchraine Pool (67.4 km), Castle Grant Beat No 2, until 17 July. Movements after this date became erratic. The tag was found on the river bank near Grantown by an angler and returned on 5 October. It is not known whether the erratic movements recorded after 17 July were genuine. However, the behaviour of F8.88 does suggest that some summer salmon reach the Tulchan and Grantown area and may progress further up stream to spawn.

Of the June fish, F11.88 was lost while F14.88 was tracked to the River Avon before eventual loss through tag failure.

The remaining June salmon, ie F12.88, F31.89, F32.89 and F34.89, occupied the lower beats for most of the summer. Fish F12.88, released on 20 June, progressed up stream to the Aultdearg Pool, Brae Water Beat No 3 (11.4 km), by 2 July. It remained there until 12 October when it moved up stream to Aikenway (21.6 km), when the MDD recorded at Boat o'Brig was 100 $m^3 s^{-1}$ (117% MMD). A further ascent occurred on 17 November when the MDD at Boat o'Brig was 44.1 $m^3 s^{-1}$ (90.1% MMD). It was last recorded at the mouth of the River Fiddich on 4 December.

Three salmon released on 13 June 1989 (ie F31.89, F32.89 and F34.89) showed very similar behaviour. After release, F31.89 and F33.89 reached the Boat o'Brig ALSTN (16.6 km) within 10 days, while F34.89 was much slower and took 34 days. All three remained in the Delfur Beat for the duration of the summer, F31.89 in the Sourden Pool (19.6 km), whilst F32.89 and F34.89 occupied the Collie Pot (17.2 km). Up-stream movements commenced for F31.89 on 20 September (262% MMD) and for F32.89 on 24 October (120% MMD). The fish reached Crechie Pool,

Rothes (23.2 km) and Aberlour (30.2 km), respectively. Fish F34.89 dropped down stream to the Brae Water (12.2 km) on 18 October (103% MMD). The fish were not tracked beyond these locations.

Figure 3 illustrates the migrations of the summer salmon. Whilst it is evident that these fish did not migrate as far up stream as the spring entrants, they did show the same over-all pattern of migration.

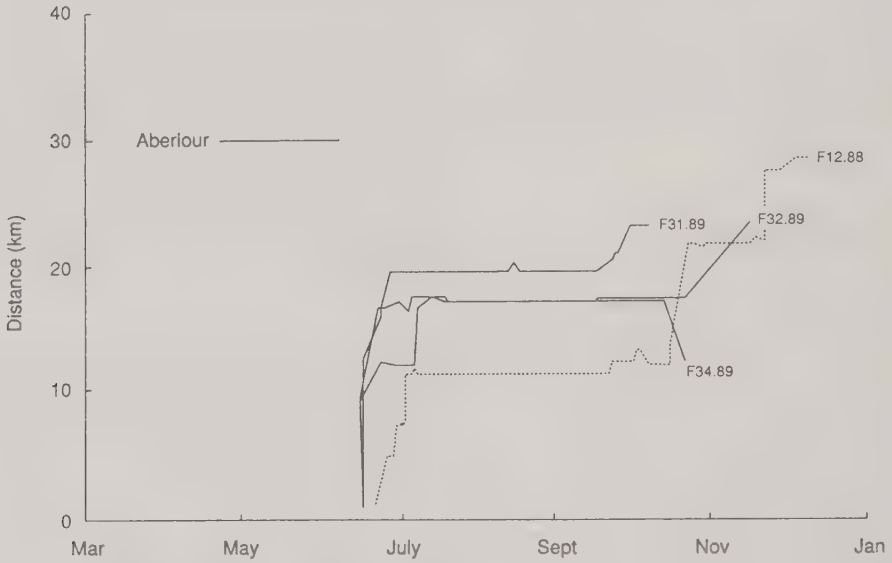


Figure 3. **The movements of summer salmon F12.88, F31.89, F32.89 and F34.89.**

The Movements of Grilse

In the previous report, Laughton (1989) described the behaviour of an early grilse, F13.88, which was released on 24 June 1988. It subsequently spawned near Newtonmore, 128 km from the sea. In order to further examine the behaviour of these fish in the Spey, 12 grilse were tagged and released into the river during June 1989. Details are given in Tables II and IV.

TABLE IV

Summary of grilse (one-sea-winter fish) showing the numbers of fish lost through tag failure, possible regurgitation, return to sea and recapture by anglers

Month	No released	No rod caught	No net caught	Tag failure	Possible regurgitation	Returned to sea	Long-term track
June	13	1	1	1	1	1	8
August	10	0	0	0	0	3	7
Total	23	1	1	1	1	4	15

Figure 4 shows the movements of the grilse released during 1989 together with the flow rates of the main stem recorded at Boat o'Brig and Grantown. It is evident from the figure that some grilse progressed considerable distances up stream. The furthest migration recorded of any fish released in the Spey was by the grilse F38.89. It was released on 16 June and after a relatively slow, interrupted ascent it reached Loch Insh (111.5 km) on 1 September. It eventually surmounted Spey Dam (146.5 km) to reach the mouth of the Allt a'Chaorainn Burn on 27 September, 150 km from the sea. Two other grilse, F44.89 and F45.89, also made long up-stream migrations

reaching the Linn of Avon (88 km) and the River Feshie (110 km) respectively.

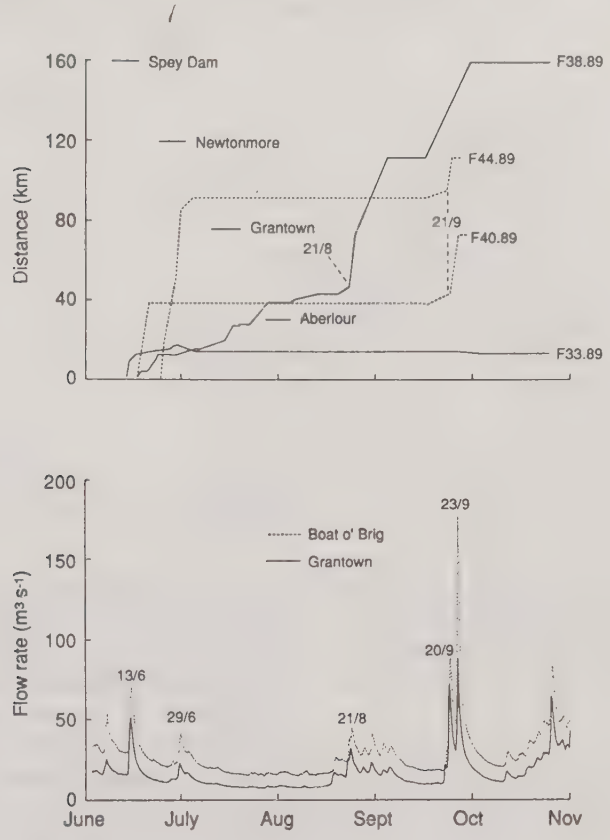


Figure 4. **Movements shown by grilse during 1989. The mean daily flow conditions at Boat o'Brig and Grantown are also shown.**

The remaining grilse F33.89, F40.89, F41.89 and F43.89 which were released during June, occupied pools much further down stream, namely the Turn Pool, Brae (13.2 km), Carron Bridge (38.3 km), the Cobble Pot, Arndilly (25 km) and the Long Pool, Knockando (42.2 km) respectively. F40.89 and F41.89 both began up-stream migrations on 21 September, during 249% MMD at Boat o'Brig, to eventually reach the Castle Grant Water (71.7 km) and the Avonmouth area (50 km). The other two grilse (F33.89 and F43.89) remained in their respective summer pools until 11 November. Both undertook small up-stream and down-stream movements throughout the year, but it was not determined whether either spawned near these pools.

A total of 10 grilse was released during August 1988. Details are given in Tables I and IV. Figure 5 shows the movements produced by grilse F17.88, F21.88 and F22.88. These grilse showed a very limited up-stream migration often remaining close to where they were released. However, during September some grilse began up-stream migrations towards spawning areas. Of this group, F21.88 progressed the furthest distance up stream reaching Avonmouth (50 km), while F20.88 and F22.88 reached Rothes (22.5 km) and Delfur (16.6 km) respectively. The others all remained further down stream.

Radio-Tagged Fish Which Returned to Sea

During 1988, three salmon (F7.88, F9.88 and F10.88) ascended considerable distances up the Spey only to return to sea between 10 and 11 days later. They reached Arndilly (26.2 km), Carron (40 km) and Aberlour (30.6 km), respectively, before returning down stream. During 1989, four fish (F2.89, F9.89, F10.89 and F42.89) showed similar behaviour reaching the Essil pool, Lower Water (2.7 km), Boat Pool, Aberlour (30.6 km), Two Stones, Delfur Beat (19.6 km) and the Bridge pool, Lower Water

(2 km), respectively, before returning down stream. The time spent by each of these fish in the Spey varied from 2 to 49 days.

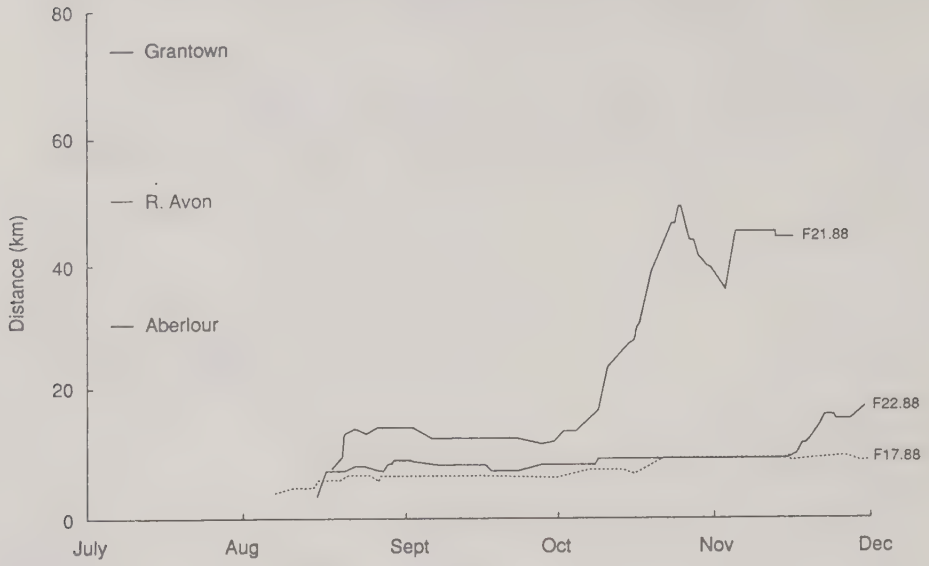


Figure 5. **Movements shown by grilse released during August 1989.**

Fish F9.89 was released into the lower Spey on 10 February and progressed up stream reaching Aberlour (30.6 km) by 20 February, remaining there until 28 February before dropping back to Delfur (18.4 km). The fish continued down stream, passing the lowest ALSTN at Brae Beat No 5 on 6 March and leaving the Spey soon after. The salmon was eventually caught by rod on the Dorback Burn, a tributary of the River Findhorn, approximately four months later on 17 July.

In addition, two other salmon, F19.89 released on 21 March and F27.89 released on 3 March, left the river during October after 208 days and 202 days respectively. During this period F19.89 had reached Avonmouth (50 km) by 16 October, while F27.89 reached Castle Grant Beat No 1 (70.5 km) before dropping back through Brae Water Beat No 5 ALSTN (9.2 km) on 19 October. No further signals were detected. It seems unlikely that these fish spawned in the Spey before moving down stream.

These results indicate that some fish may enter the Spey, but subsequently move down stream and out of the river. The capture of one of the fish (F9.89) on the River Findhorn lends support to the idea that some may subsequently enter other rivers.

Delayed Entry of Radio-Tagged Fish into the River Spey

Two fish (F19.89 and F21.89) released on 21 and 28 March respectively, returned to sea after tagging, but subsequently re-entered the river at a later date. Extensive surveys of the lower reaches provided no signals for either fish until 4 and 12 April respectively, when both were recorded ascending by the Brae Water Beat No 5 ALSTN (9.2 km), the lowest ALSTN on the system.

Summary of Salmon and Grilse Movements

Figure 6 shows tracks for multi-sea-winter fish and grilse released during 1988 and 1989. The estimated spawning areas are shown in Figure 7.
It is evident from Figure 6 that the pattern of movement shown by the spring salmon falls into four distinct phases. Firstly, there is a phase of up-stream ascent. Secondly, there is a period of relative quiescence, often spent at a particular location during the summer months, which is occasionally interrupted by further movements up stream. Thirdly, during late autumn an up-stream migration takes place to a spawning site. Finally,

the fish may move down stream after spawning as a kelt. Although the summer salmon did not migrate as far up stream as the spring entrants, they did show the same over-all pattern of migration.

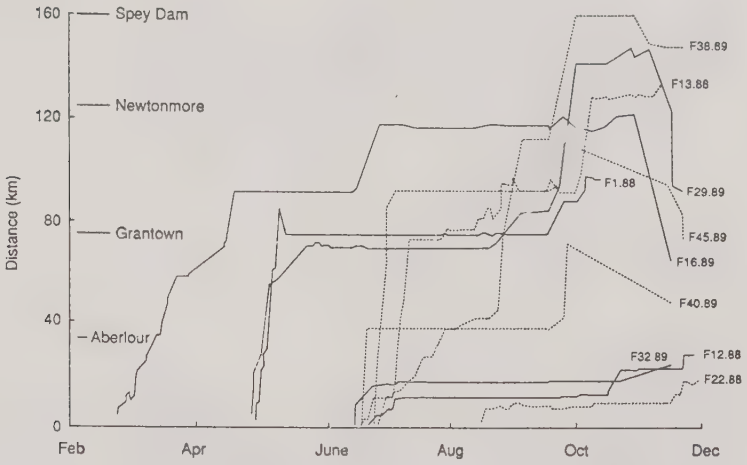


Figure 6. **Summary migrations of River Spey salmon and grilse. The earlier entrants within each sea age class progress further up stream than those ascending later in the year.**

The eventual spawning areas of the spring salmon and summer salmon are shown in Figure 7. The spring salmon spawn in the upper areas of the river while the summer salmon remain in the lower reaches.

Grilse appear to show an over-all pattern of migration similar to that of the multi-sea-winter fish. An ascent phase was followed by a period spent in a holding pool and then, towards the end of autumn, an up-stream migration to spawning sites occurred.

From Figures 6 and 7 it is evident that the eventual destinations for grilse differ throughout the season. Some of those entering during June reached the upper areas of the river and its tributaries, while those entering during August remained in the lower beats, often spawning close to their release point.

Timing of Fish Movements

During their up-stream migration fish did not move continuously but often stopped in holding pools during the day and commenced migrations at night. Timing of movements were recorded during the year by ALSTNs placed along the length of the river. In this way the period of the day when the fish were migrating was recorded. All movements, up stream or down stream, were included in the analysis. The results are presented in Figure 8.

During February and March (Fig. 8a) there is no clear trend. The most noticeable pattern occurred during April and May (Fig. 8b), where most movements took place at night, typically beginning around dusk and finishing near dawn. Whilst there is some suggestion that this pattern exists during June and July (Fig. 8c), with most of the movements recorded during the early hours of the morning, after July no clear pattern is evident.

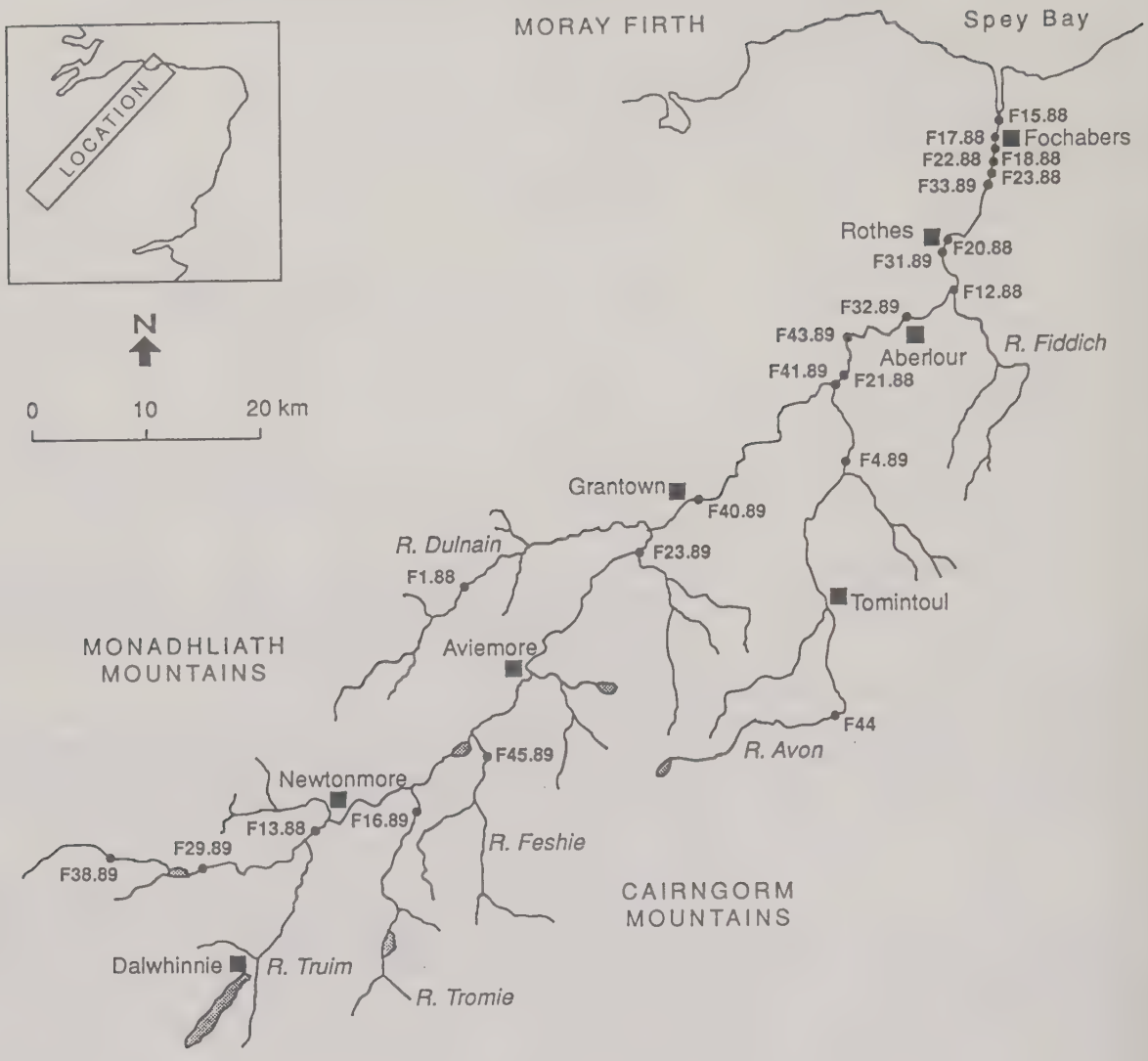


Figure 7. **The River Spey and its tributaries showing the eventual spawning positions of the radio-tagged salmon and grilse.**

Movements during daylight

From the data presented in Figure 8 it is evident that fish are predominantly active at night, although daylight movements were also recorded. Although many of these movements were by fish continuing their migrations after dawn, some were recorded recommencing migrations during daylight. Table V summarises information on those fish that recommenced movements during daylight together with the prevailing flow data, the maximum daily discharge and the relative percentage of the mean monthly discharge (% MMD).

From the data presented in Table V it is evident that there is a close association between daylight migrations and increases in river discharge; of the 30 daylight movements, 27 (90%) occurred during spate conditions whilst only three (10%) took place when there was no spate.

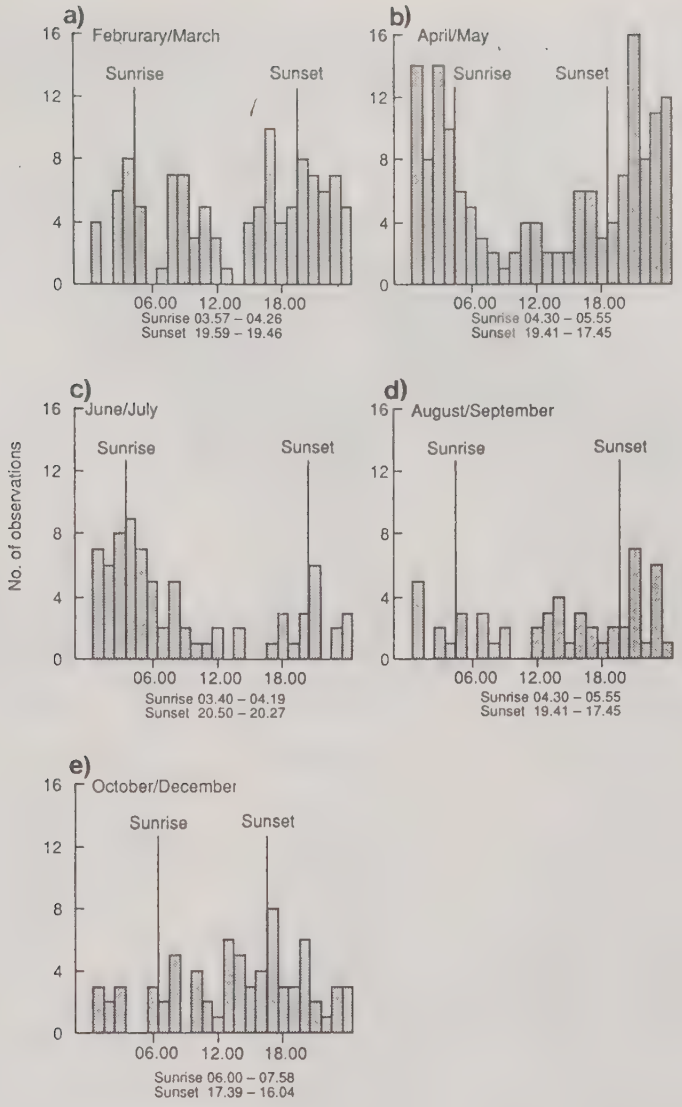


Figure 8. **The time of day when fish were active. Movements up stream and down stream and from all phases of fish migration are included. The range of sunrise and sunset times for each sample period are shown.**

From the data presented in Table V it is evident that there is a close association between daylight migrations and increases in river discharge; of the 30 daylight movements, 27 (90%) occurred during spate conditions whilst only three (10%) took place when there was no spate.

Behaviour during the ascent phase

Figure 9 shows the mean time of ascent for each monthly group of fish to reach the Brae Water Beat No 5 ALSTN (9.2 km) and the Boat o'Brig ALSTN (16.6 km). Figure 10 shows the mean distance progressed by each group during the first 15 days after release. It is evident from the results shown in Figures 9 and 10 that there are differences in the up-stream progress of each monthly group.

Spring salmon ascending during February and March make less progress during the first 15 days than those ascending during April, and this is also reflected in the times taken by these groups to reach the Boat o'Brig ALSTN. From Figure 10 it is evident that the salmon released during May showed similar progress to those ascending during April; however, three of the four salmon released during May returned to sea 10 or 11 days after

TABLE V

Observations on fish which recommenced up-stream migrations during daylight after a period of >5 days in a holding position. The maximum daily discharge and the percentage MMD are shown along with the time of sunrise and sunset during the period

Fish	Date and time of movement	Nearest gauging station	Max daily discharge (m^3s^{-1})	Percentage MMD	Sunrise (GMT)	Sunset (GMT)
1.88	03.05 (1350-1505)	Boat o'Brig	136.0	231	0430	1958
	07.05 (1600-1655)	Boat o'Brig	76.6	130	0422	2006
3.88	03.05 (1015)	Boat o'Brig	136.0	231	0430	1958
6.88	02.05 (1500-1525)	Boat o'Brig	140.0	238	0432	1956
	26.05 (1555-1900)	Boat o'Brig	41 7	71	0348	2041
9.88	15.06 (1115-1120)	Boat o'Brig	25.9	102	0404	2024
13.88	06.07 (1820-1836)	Boat o'Brig	89.5	164	0340	2102
	21.08 (1540-1606)	Grantown	147.0	339	0459	1940
	27.08 (1445-1456)	Grantown	73 4	170	0510	1925
	28.09 (1425-1436)	Grantown	34.5	111	0613	1801
3.89	12.02 (1115-1200)	Boat o'Brig	66.5	69	0716	1713
7.89	15.02 (1140-1200)	Boat o'Brig	234 9	243	0711	1718
9.89	15.02 (1055-1130)	Boat o'Brig	234 9	243	0711	1718
10.89	08.04 (1555)	Boat o'Brig	54.7	101	0524	1841
14.89	02.03 (1055-1140)	Boat o'Brig	189 9	159	0642	1744
16.89	03.03 (1220-1225)	Boat o'Brig	129 6	108	0640	1746
	17.10 (1350-1440)	Grantown	26.5	98	0625	1705
12.89	23.09 (1115-1145)	Grantown	91 7	449	0548	1756
26.89	12.04 (1415-1435)	Boat o'Brig	86 6	160	0514	1849
27.89	01.04 (1300-1400)	Boat o'Brig	109 3	202	0537	1832
	24.09 (1535-1730)	Boat o'Brig	86.1	256	0636	1562
29.89	27.04 (1210-1220)	Boat o'Brig	54 2	100	0444	1912
	02.05 (1315-1325)	Boat o'Brig	86 6	166	0435	1920
	20.08 (1335)	Grantown	32.4	230	0457	1909
30.89	28.04 (1545-1550)	Boat o'Brig	55.4	104	0442	1914
31.89	14.06 (1140-1150)	Boat o'Brig	69 7	218	0350	2011
38.89	21.08 (1145-1245)	Grantown	32.7	232	0458	1908
40.89	21.09 (1550-1600)	Boat o'Brig	83 6	249	0545	1756
41.89	21.08 (1605-1715)	Boat o'Brig	44 8	188	0458	1980
	21.09 (1145-1335)	Boat o'Brig	83 6	249	0545	1756

release. This could account for the slower progress shown in Figure 9. The June grilse showed more rapid progress than the June salmon whilethe August grilse did not progress much beyond the Brae Water Beat No 5 ALSTN.

In June, salmon do not progress to the upper areas of the river but remain in areas down stream from Grantown. However, the grilse showed a wide range of destinations; some progressed to the upper tributaries whilst others remained in the lower reaches. These two groups were analysed separately and the results are shown in Figure 11. Grilse destined for the upper reaches progressed much further up stream during their first 15 days than those remaining in the lower reaches. The progress made by the

grilse destined for the upper reaches was similar to that shown by salmon ascending during April and May.

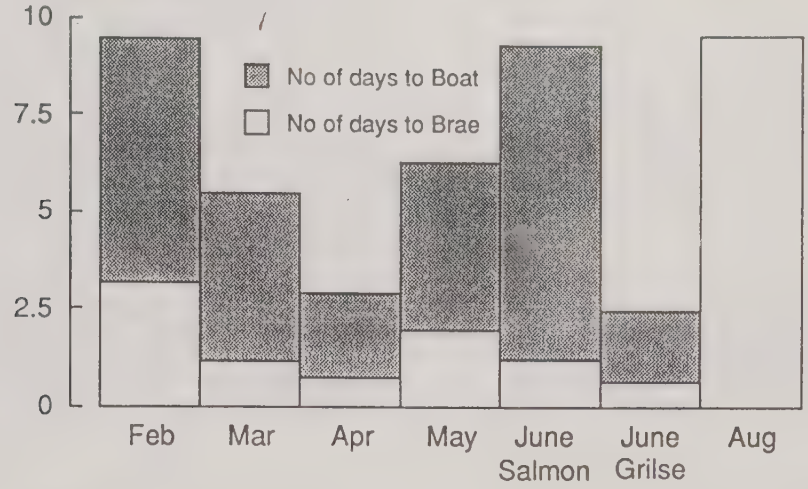


Figure 9. **The average time taken by each monthly group of fish to reach the Brae Water Beat No 5 ALSTN (9.2 km) and the Boat o'Brig ALSTN (16.6km). Salmon and grilse ascending during June are shown separately.**

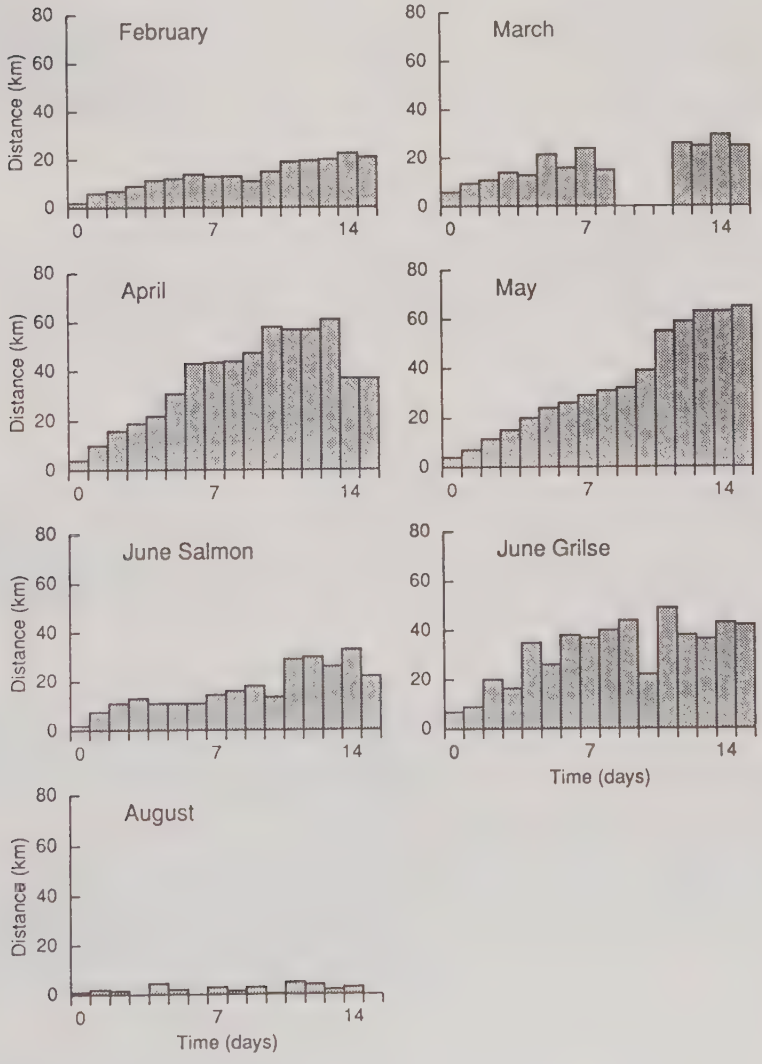


Figure 10. **The average distance moved by each monthly group of fish during the first 15 days of the ascent phase.**

Movements after the first ascent

During early migration, fish movements were predominantly crepuscular and nocturnal and appeared to take place regardless of the prevailing flow conditions (Fig. 8). However, within this migration daylight movements were recorded which correlated closely with increased flow rates (Table V).

For much of their riverine migration the adult fish remained at a fixed location in the river; however, this quiescent period was often interrupted by a further up-stream movement to a new holding position. These later movements were analysed to determine if there was any relationship with changing flow rates. Where fish showed a discontinuous up-stream migration, such as F2.88 and F38.89, data from the recommencement of progress were included if a period of greater than five days was spent in a holding position. The movements analysed were for main stem movements between Boat o'Brig and Grantown; tributary movements were excluded.

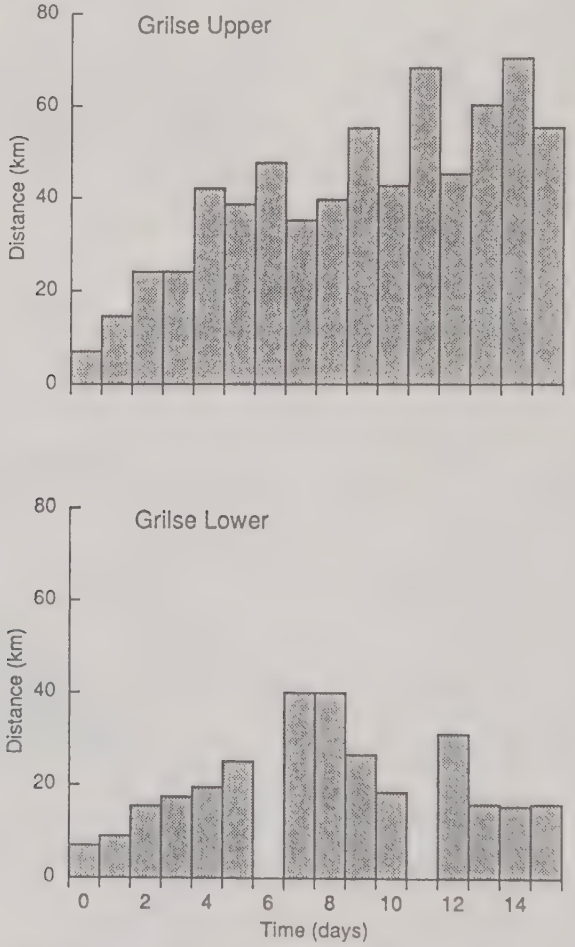


Figure 11. **The average distance moved during the first 15 days of the ascent phase by grilse released during June. Grilse which progressed to the upper reaches are shown separately from those that remained in the lower reaches.**

Figures 12a and 12b show the frequency of mean daily flows recorded at Boat o'Brig from May to November 1988 and from March to October 1989. The mean daily flows at which fish were recorded as moving were determined, and are indicated in Figures 12 a and 12b.

From the results presented in Figures 12a and 12b, it appears that salmon movements occur over a wide range of flows. Only during July 1988, June 1989 and August 1989 were the flows at which fish commenced

movements significantly greater than the over-all range of flows available during the month (Mann Whitney test $p < 0.05$; Zar, 1974).

Figure 12 shows all the movements which occurred after the fish had been stationary for a period of five days or more. The analysis can be refined further to examine the flows associated with the first movement of fish away from a holding position. Table VI shows the numbers of these movements recorded during 1988 and 1989, and the percentage of days which had flow rates higher than the monthly mean.

It is evident from Table VI that most of these movements were associated with higher flow rates than the mean monthly discharge (82% during 1988 and 78% during 1989). The percentage of movements is also higher than the number of days associated with spates during the period.

TABLE VI

The percentage of fish migrations which recommenced after a period of >5 days in a holding pool, and which were associated with increased discharge. The percentage of days associated with spates during the period of movements is also shown.

Year	Total no of movements	Total no of movements associated with higher than average flow rates	Percentage (%)	Percentage of days associated with increased discharge (%)
1988	11	9	82	55
1989	18	14	78	44

The previous analysis shows some evidence that salmon commence movements during periods of higher flow rates. Figures 13a-d show several spate events from 1989 at Boat o'Brig, Grantown, and from two tributaries the Avon and the Tromie. The timing of fish movements are also shown above the hydrograph.

Figure 13 shows that although fish movements were often associated with spates, the fish did not always move at the maximum discharge level. Some movements occurred before the peak as levels began to rise, as in for example F28.89 (Fig. 13a) and F23.89 (Fig. 13d). Most movements occurred as the discharge levels were falling whilst others like that of F12.89 for example (Fig. 13a) appeared not to be related to any spate incident.

The Behaviour of Salmon and Grilse Ascending Tributaries

The behaviour of fish ascending the River Avon

In the previous report, Laughton (1989) described the movements of salmon F14.88, which entered the Avon during spate conditions before it was eventually lost through probable tag failure. During the 1989 tracking programme a total of five fish, three spring salmon (F4.89, F12.89 and F28.89) and two grilse (F41.89 and F44.89) made excursions to the tributary confluence, whilst three of these fish (F4.89, F41.89 and F44.89) subsequently entered the tributary. The behaviour of these fish is worth describing in some detail.

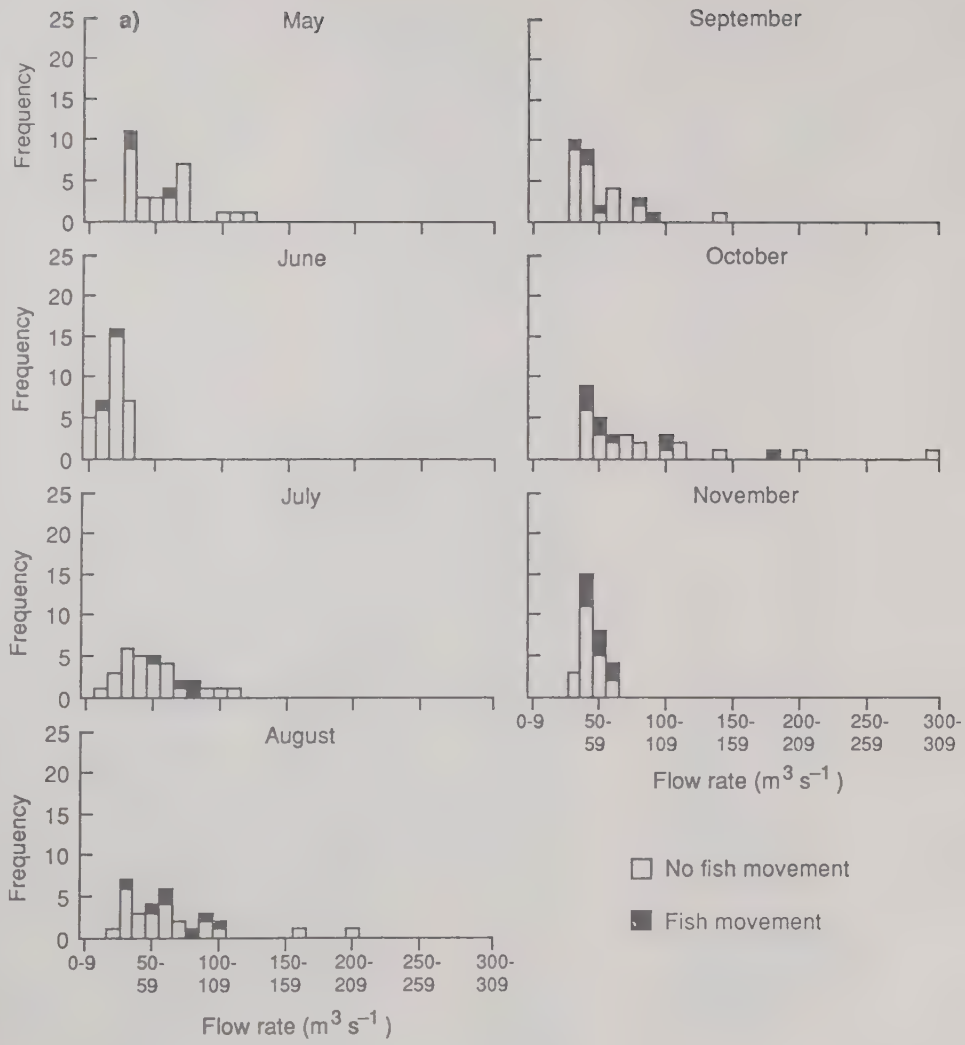


Figure 12 a). **Frequency distribution of the 1988 river discharges ($m^3 s^{-1}$) at Boat o'Brig showing periods of fish movement and of no fish movement.**

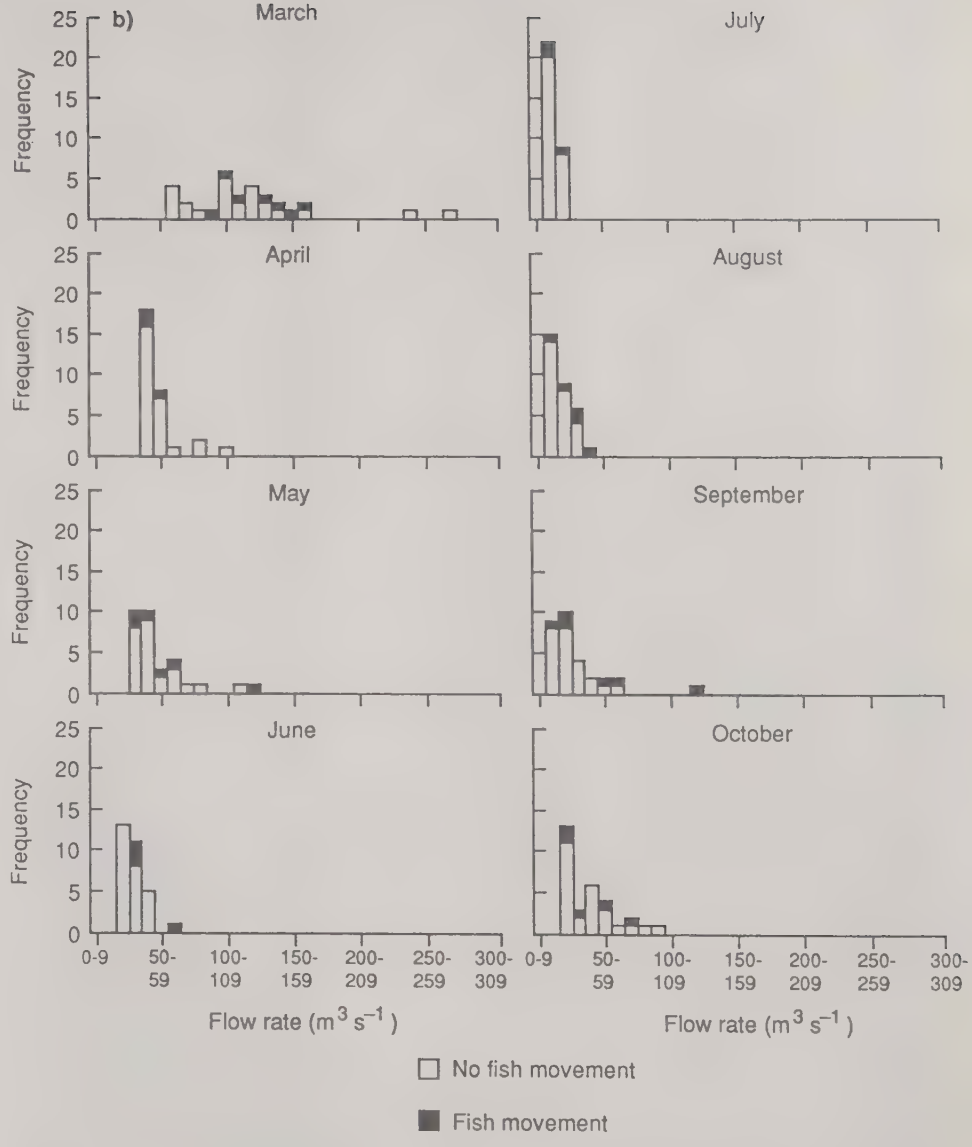
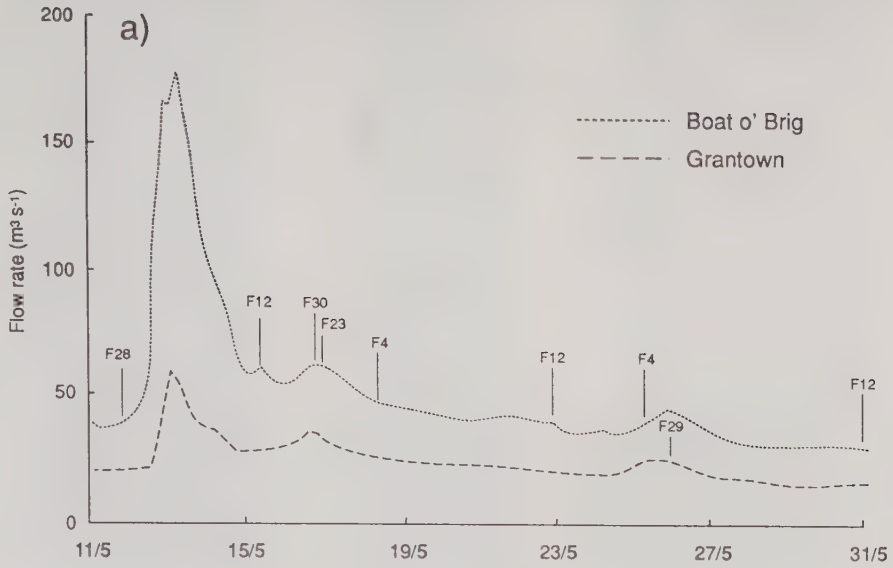
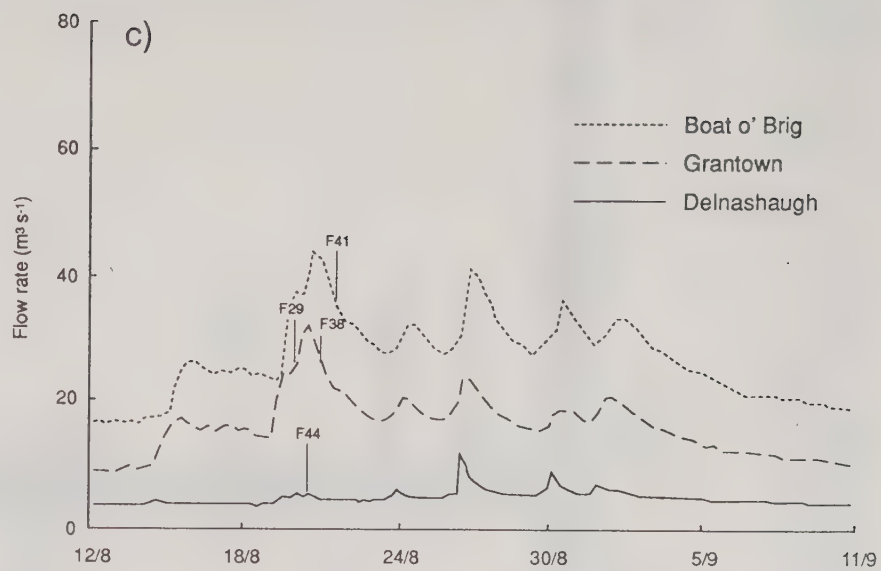
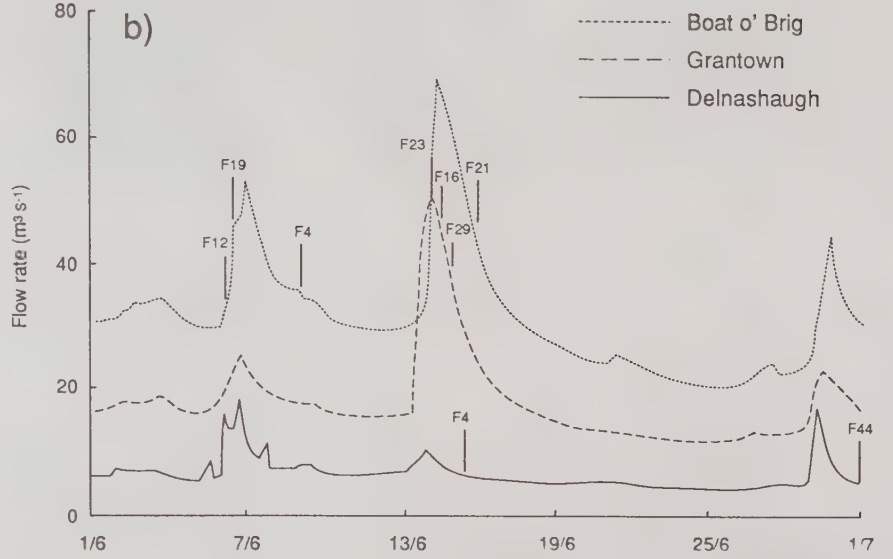


Figure 12 b). **Frequency distribution of the 1989 river discharges ($m^3 s^{-1}$) at Boat o'Brig showing periods of fish movement and of no fish movement.**







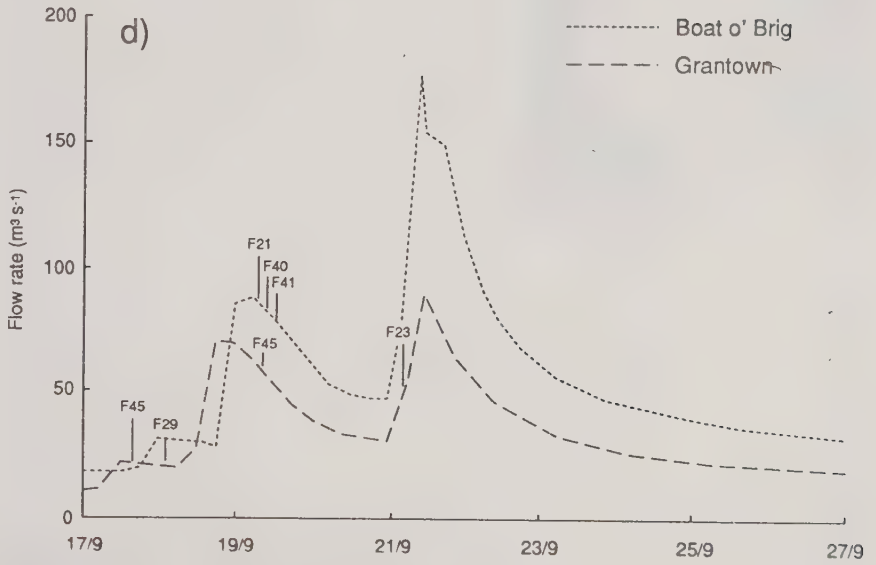


Figure 13 a-d). **Hydrographs from Boat o'Brig, Grantown and Delnashaugh on the River Avon showing spate events and the movements of individual fish.**

Figure 14 shows a diagram of the area around the confluence and the positions of the ALSTNs at Avonmouth, Ballindalloch, Dalmench and lower Tulchan. The position of the NERPB gauging station at Delnashaugh is also shown.

Figure 14. **Diagram of the River Avon confluence area, showing the positions of the ALSTNs and the Delnashaugh gauging station.**

Although fish F12.89 reached the confluence of the Avon on 7 May, no positive record of it entering the tributary was obtained. It subsequently dropped back down stream reaching the Brae Water Beat Number 5 ALSTN (9.2 km) on 12 May before making a short up-stream migration to the Holly Bush pool, Delfur (19.7 km), where it remained until contact was lost through tag failure. Fish F28.89 released on 26 April was last recorded by the Avonmouth ALSTN on 17 May. No further signals were received for F12.89 or F28.89 in either the main stem or throughout the length of the Avon, despite extensive aerial surveys.

Figure 15 shows the movements of F4.89 which was released on 8 February. Also shown are the hourly flow rates recorded at Boat o'Brig and Delnashaugh. The up-stream progress shown initially by F4.89 was similar to that shown by other radio-tagged spring salmon. It reached the Sourden Pool, Delfur (20.9 km) on 20 February and remained there until mid April.

F4.89 made four approaches to the tributary. The first began from the Collie Pot, Arndilly (24.8 km) soon after 8 May. The fish reached the Avonmouth ALSTN on 18 May but did not appear to enter the tributary. This movement may have been stimulated by a spate occurring in the tributary on 12 May. The fish subsequently dropped back to Island Roary, Knockando (41 km), where it remained before ascending to enter the Avon on 24 May. It remained in the Avon near Delnashaugh Hotel (52 km) before

returning down stream to eventually reach the Boat o'Brig ALSTN (16.6 km) on 8 June.

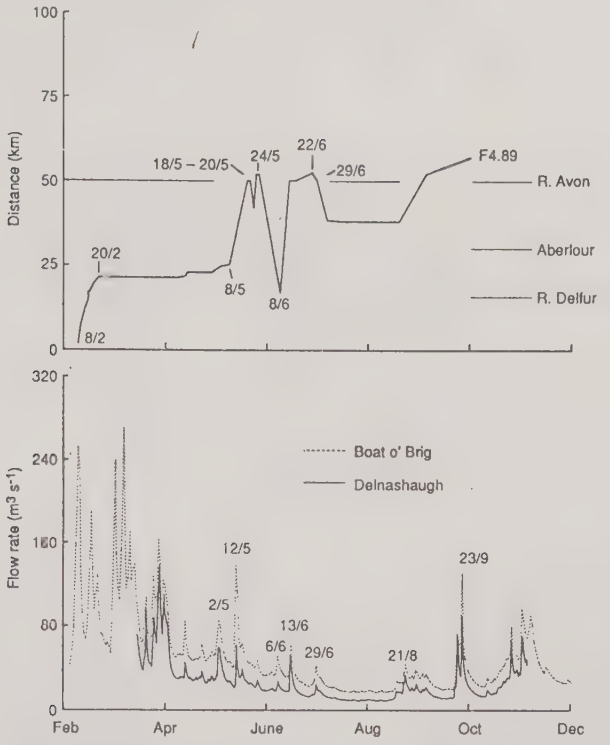


Figure 15. **The movements of F4.89 (a spring salmon) which entered the River Avon. The mean daily flows at Boat o'Brig and Delnashaugh are also shown.**

A further ascent began on 8 June reaching the Avonmouth ALSTN on 12 June. Increased discharges were recorded at Boat o'Brig (MDD 49 $m^3 s^{-1}$, 153% MMD) on 6 June, just prior to the ascent. A small spate of 11.2 $m^3 s^{-1}$ (167% MMD) was recorded during 13 June on the Avon and this may have encouraged the entry to the tributary. However, the exact time of entry was not recorded.

The fish returned down stream to the main stem on 29 June when the MDD at Delnashaugh was 8.4 $m^3 s^{-1}$ (125% MMD). It remained at Carron Bridge (38 km) until 17 August. From mid August onwards the signals from the tag became very weak and accurate data for movements were not obtainable. A final signal from the fish was detected in the River Avon on 27 September near Glenballoch (56.9 km).

Figure 16 shows the tracks for F41.89 and F44.89, together with the hourly flow rates recorded at Boat o'Brig and Delnashaugh.

Fish F41.89 and F44.89, both grilse, were released on 23 June. From Figure 16 it is clear that they showed very different rates of up-stream progress.

Fish F44.89 progressed rapidly up stream reaching Avonmouth ALSTN (50 km) in 5.2 days. It was recorded ascending the tributary on the Dalmenach ALSTN on 1 July, the mean daily discharge at Delnashaugh on 29 June being 14.2 $m^3 s^{-1}$ (211% MMD). As tributary levels dropped, the fish returned to the main stem, settling at the mouth of the Cally Burn (45 km). It re-entered the Avon on 20 August when the maximum flow rate at Delnashaugh was 5.8 $m^3 s^{-1}$ (136% MMD). Contact was lost until 27 September when it was located at the Linn of Avon, 88.4 km from the sea

and 38.4 km from the confluence. It was tracked until late October and probably spawned in the upper area of the Avon.

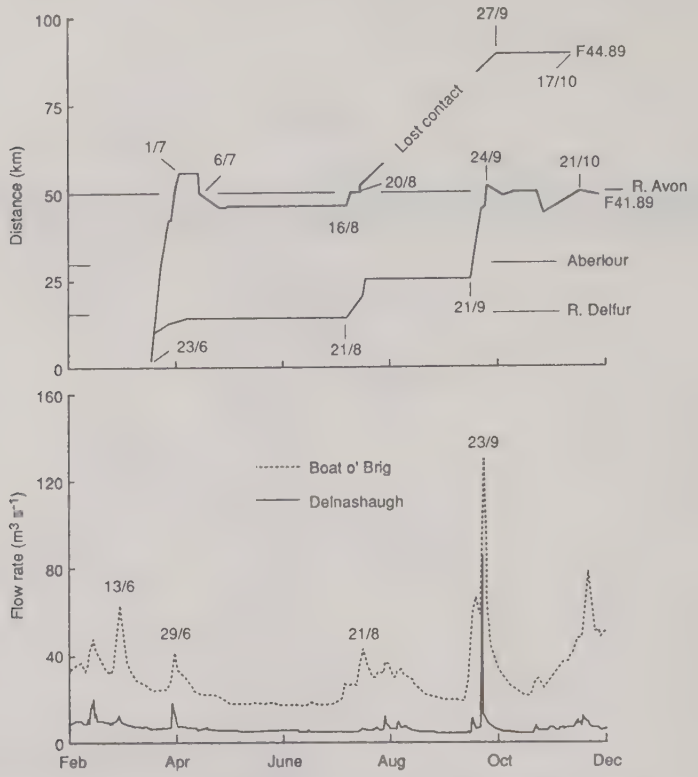


Figure 16. **The movements of F41.89 and F44.89, both grilse, which ascended the River Avon. The mean daily flows at Boat o'Brig and Delnashaugh are also shown.**

Fish F41.89 was released on the same day as F44.89 but showed a slower migration. It settled in the Turn pool, Brae Water (13.8 km) until 21 August when it moved up stream to the Cobble Pot, Arndilly (25 km). The fish progressed towards the Avon on 21 September during increased flows, the MDD at Boat o'Brig being 65.7 m^3 s^{-1} (195% MMD). River flows in the Avon peaked at 85.9 m^3 s^{-1} on 22 September (1,525% MMD) and F41.89 ascended soon after. It was recorded on the Ballindalloch ALSTN on 24 September. It returned to the main stream on 27 September and eventually dropped to Tamdhu, Knockando (43.6 km). A final up-stream migration in conjunction with a spate of 12 m^3 s^{-1} (180% MMD) occurred on 21 October, and it appears that grilse F41.89 spawned near the confluence area.

Thus, it is evident from the behaviour of F4.89 that some spring salmon may spend much of the early season in beats well down stream from the Avon, and make repeated ascents to the confluence. In all, four ascents were made by F4.89. Similar behaviour was shown by F44.89, a grilse, which made an early entry to the Avon, but dropped back to the main stem before re-entering later in the year.

The general behaviour of fish ascending tributaries

A total of nine fish entered tributaries of the Spey during the study period. Details of each fish, along with the tributary they entered and the timing of their movements, are shown in Table VII. The prevailing riverconditions are also given, including where possible the percentage mean monthly discharges. However, in the Rivers Feshie and Calder flow data are not available, so data from the nearest main stem stations are shown.

TABLE VII

The dates fish entered various tributaries of the Spey. The prevailing flow conditions during the entry period are also shown. Because flow rates were not recorded in the Feshie and the Calder, data from the nearest main stem gauging stations (Kinrara and Invertruim) are given

Fish No	Tributary	Date of Entry	Prevailing flow conditions
1.88	Dulnain	12-20.09	13.09 - 331% MMD Balnaan
6.88	Dulnain	14-16.07	14.07 - 377% MMD Balnaan
13.88	Calder	25.10	25.10 - 158% MMD Invertruim
14.88	Avon	06.07	05.07 - 367% MMD Delnashaugh
4.89	Avon	24.05	24.05 - 85.6% MMD Delnashaugh
	Avon	15.06	13.06 - 167% MMD Delnashaugh
16.89	Tromie	20.09	20.09 - 342% MMD Tromie Bridge
	Tromie	17.10	No spates recorded
41.89	Avon	24.09	24.09 - 187% MMD Delnashaugh
44.89	Avon	29.06-01.07	29.06 - 211% MMD Delnashaugh
	Avon	20.08	20.08 - 136% MMD Delnashaugh
45.89	Feshie	21.09	21.09 - 311% MMD Kinrara

From the details presented in Table VII, fish showed a tendency to enter tributaries either during elevated discharges or soon after. Only two entries were made in the absence of a spate, namely F4.89 to the Avon on 24 May, and F16.89 to the Tromie on 17 October. Further analysis of the River Avon hydrograph showed there was a slight increase in the tributary flow levels, from 8.24 $m^3 s^{-1}$ on 23 May to 10.75 $m^3 s^{-1}$ on 24 May. Daily movements were not obtained before 17 October for F16.88, so accurate details of the entry time of this fish were not obtained.

Radio-Tagged Fish Caught by Anglers

During 1988 and 1989, 10 spring salmon and one grilse were caught by anglers on the River Spey (see Tables I and II). Anglers fishing at Orton (13.8 km) and at the Aberlour Association Water (33.1 km) each accounted for three, Arndilly (25.7 km) accounted for two, while Delfur (16.6 km), Rothes (23 km) and Castle Grant Beat No 1 (70 km) caught one each. One other spring salmon (F9.89) was landed on the Dorback Burn, a tributary of the River Findhorn.

With a sample size of only 69 tagged fish estimates of exploitation rates are not justified. However, some information can be gained from the recaptures.

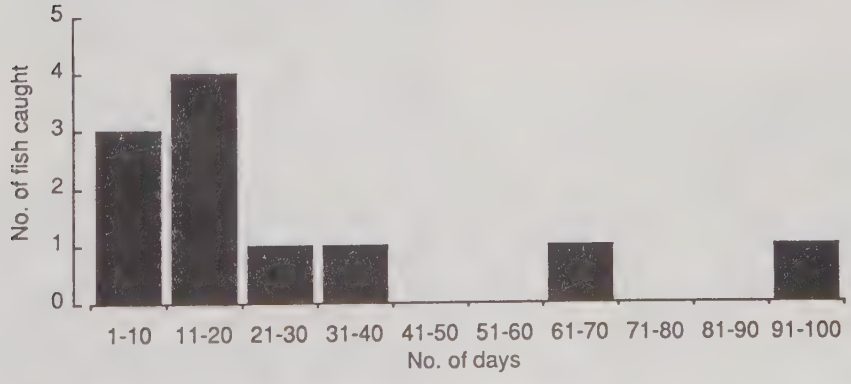


Figure 17. **The number of days from release to recapture for radio-tagged fish which were caught by anglers.**

Figure 17 shows the number of days between the release of a radio-tagged fish and its subsequent recapture by an angler. Most of the fish (82%) were caught within 40 days of release, but two (F8.89 and F17.89) were

caught after 69 and 97 days respectively. The average time of recapture is 15 days if these two fish are excluded, and 28 days if they are included.

Figures 18a and b show the up-stream progress made by each of the rod caught fish. The results indicate that fish were taken either during their up-stream ascent or between 2 and 11 days after their final recorded movement. The obvious exceptions are F8.89 and F17.89 which were caught much longer after release. However, F8.89 was recorded on the Arndilly Farm ALSTN (24.9 km) as recommencing up-stream movements just prior to being caught in the Jocks Tail Pool, Arndilly (25.5 km). Fish F17.89 also showed up-stream movements just before recapture.

Discussion

Time of Entry and Movement Up Stream

Spring salmon migrate to, and subsequently spawn in, the higher reaches of the Spey. These areas include the upland tributaries such as the Dulnain, the Feshie, the Tromie or in the main stem itself. Multi-sea-winter salmon entering during the summer months do not progress as far up stream, tending to occupy the lower stretches of the river such Delfur, Arndilly and Knockando and eventually spawning close to these areas.

The pattern is repeated by grilse entering the river between June and the end of the season. Some of the earlier entrants reach the headwaters, while later entrants remain in the lower reaches.

The pattern of entry shown here for spring salmon ascending the Spey has also been described by Hawkins and Smith (1986) for the Aberdeenshire Dee, and concurs with the general pattern outlined by Milner (1990). Some grilse tagged and released during June in the Dee have also shown major up-stream migrations of between 60 and 85 km (G.W. Smith, pers. comm.). The relationship is complicated, however, by spring salmon entering during February or March and which are destined for the River Avon. These fish (eg F4.89, Fig. 15) may remain in the lower beats of the main river for much of the season. They may also make several ascents to the tributary but do not always remain in it, choosing instead to return to the main stem. This behaviour is in agreement with Webb (1989), who reports that salmon in the River Tay may remain below a tributary and make several excursions into it, only to return down stream to the confluence area soon after.

Several other rivers in which seasonal differences in the timing of entry for different salmon sea-age classes include the Tay (Struthers, 1984), the North Esk (Shearer, 1990) and the Miramichi in Canada (Saunders, 1967). However, these studies gave no indication of the final spawning positions for each of the sea-age classes.

From the present study it appears that the timing of river entry is linked to the eventual spawning area within the river as a whole. The pattern is consistent within the two age classes (1SW and 2SW) examined here. Early entrants from either sea-age class progress further up stream than later ones. Saunders (1967) suggested that the timing of fish entry is related to the distance travelled to reach the spawning site. However, it is unclear why multi-sea-winter salmon enter during the spring, when grilse, which will eventually spawn in the same area, delay their entry until the summer. If a spring salmon had remained in the sea, presumably it would have increased its size and so its reproductive capacity. This question has yet to be resolved.

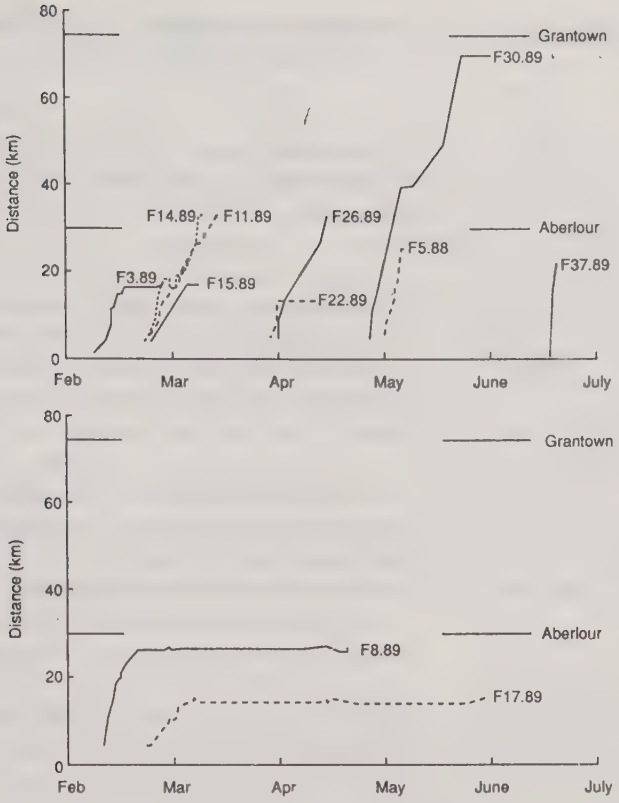


Figure 18. **The movements of radio-tagged fish which were subsequently caught by anglers.**

Up-stream migrations in the lower reaches of the Spey

The transition from sea water to fresh water is likely to be an important phase in the up stream migration of salmon. Webb (1990) suggested that salmon making a commitment to enter the River Tay do so rapidly in a single movement, beginning from the estuary and ending above the head of tide. This movement typically lasts less than 24 hours, and can take place at any time of day over a wide range of discharges. Other authors including Potter (1988) and Phillips (1989) also found evidence of rapid ascents from sea water to fresh water. Yet other workers have shown that salmon may remain for longer periods in the estuary (Stasko, 1975; Brawn, 1982).

The River Spey has little or no estuary (Thompson, 1979) and the sweep net fishery operates almost entirely in fresh water. During this study there was no opportunity to examine the initial entry of fish into the river.

Webb (1989) and Hawkins and Smith (1986) suggested that following entry to fresh water the subsequent ascent phase is stepwise rather than continuous. Movements are predominantly nocturnal, typically beginning around dusk and ending at dawn, with the fish remaining in a holding position (often a pool) during the day. Results from the Spey tend to support these findings. This pattern is best illustrated by salmon ascending during April and May; during other months it is not so clear. After July most of the movements observed were of fish recommencing movements, many of which were related to increases in river discharge.

With the exception of daylight movements, this migration phase proceeded regardless of the range of prevailing flow conditions, in agreement with the findings of both Webb (1989) and Hawkins and Smith (1986).

For one spring entrant (F29.89, see Fig. 2) migration from the summer holding pool to the spawning site was longer than the earlier up-stream

migration. However, fish generally completed most up-stream progress during the first phase.

The radio-tagged spring salmon ascending during February and March progressed less up stream during the first 15 days of migration than those ascending in April.

Salmon entering a river during February or March are likely to experience much higher flow rates combined with much lower river temperatures than those entering during the summer. Together, these conditions may affect the ability of salmon to progress up stream. In April, as the river begins to warm, fish may find it easier to ascend. Work on the spring salmon on the Spey and the Tay by Menzies (1939) showed that although salmon entered these rivers when the temperature was as low as 1°C, they seldom progressed more than 15 to 20 km up stream. An improvement in the ability of fish to surmount obstructions such as waterfalls and dams when the river water temperature rises above 5°C is well documented (Pyefinch, 1955; Jackson and Howie, 1967; Jensen *et al.*, 1986). Thus, it is possible that the ability of fish to make up-stream progress in the early months of the year is limited by the prevailing river temperatures and flow rates. During June the picture becomes more complex with both salmon and grilse ascending the river. The June salmon tend to remain in the lower reaches to spawn, as do some of the grilse, while other grilse progress further up stream. Thus, the initial rate of up-stream progress is related to the ultimate destination of the fish.

Quiescent phase

The duration of the first ascent and the distance travelled up stream varied throughout the year. Earlier entrants progressed further up stream than later fish of the same sea-age. The fish then entered a quiescent phase, occupying a particular pool for much of the summer. Little or no movements were shown during this period. However, some fish made further migrations during this quiescent phase to occupy a new holding location; such migrations were often associated with increases in river discharge. Webb (1990) made similar observations for fish ascending the River Tay.

Further migration towards spawning areas

Towards the end of autumn, all fish showed a further migration culminating in spawning. This autumn migration was often associated with an increase in river flow. River Spey fish either entered tributaries or remained in the main stem to spawn. The exact locations of spawning redds were not determined but the likely areas could be estimated. Behaviour during this period generally consisted of an up-stream migration of varying length followed by a period of up-stream and down-stream movements, sometimes over considerable distances. The salmon and grilse near the upper end of the river tended to show longer migrations to spawning areas, whilst those remaining in the lower reaches of the river remained close to their release sites. A full description of salmon spawning behaviour is given by Webb and Hawkins (1989) for the Girnock Burn, a tributary of the Aberdeenshire Dee.

Behaviour of kelts

A final migration down stream after spawning was observed for several 1989 fish but little quantitative data on the movements of kelts were obtained. Few studies have been carried out on the behaviour of kelts. Webb and Hawkins (1989) gave some details of down-stream migrations after completion of spawning in the Girnock Burn. They showed that of the tagged fish, more females survived spawning than males and that females

leave the spawning area more quickly. Males very often remained on the spawning grounds until they died.

Rod-caught fish and straying behaviour

The number of salmon and grilse caught by anglers during the two year study was higher than anticipated. In total, 11 spring salmon and one grilse were caught during the two years. Although the sample size involved is too small to allow an estimation of angler exploitation rates for the Spey, the catches do provide some information on when migrating salmon are most vulnerable to capture. Most of the rod-caught fish were taken during their first ascent phase (see Fig. 18a), on average 15 days after release. The two others (see Fig. 18b) were caught after longer periods but soon after they had recommenced up-stream movements.

These results concur with Solomon (1988) and Clarke and Purvis (1990) who showed that most salmon were caught within 15 days of entry on the Hampshire Avon and the Tywi in Wales, respectively. Mills *et al.* (1986) suggested that salmon may be more catchable soon after entry into the Burrishole fishery.

During the two year study a few fish showed behaviour which may be deemed unusual. Several fish entered the Spey only to return down stream to sea; one of these (F9.89) was eventually caught by an angler on the River Findhorn. Calderwood (1922) cited several examples of salmon tagged in one locality which reappeared in another. The most notable of these was a "fresh" fish released in the lower reaches of the Spey during November 1921, which reappeared at Warwick on the River Eden in June 1922, some 620 miles (about 1,010 km) away. Some fish tagged in the Aberdeenshire Dee estuary have been recaptured in the Spey and Tay catchments, though these salmon did not appear to progress far up the Dee (G.W. Smith, pers. comm.). Other authors, including Clarke and Purvis (1990) and Solomon (1988), give examples of non-native salmon ascending one river only to return down stream and progress to another one. From a smolt tagging programme carried out on the rivers draining into the Severn Estuary, Swain (1982) showed 4% of returning adults ascended non-natal rivers. However, Stasko *et al.* (1973) suggested that straying between rivers is not a widespread phenomenon.

Movements in Relation to River Flow

Several authors, including Huntsman (1945), Hayes (1953) and Banks (1969), concluded that increases in discharge play a major role in encouraging salmon to migrate up stream. Using results from a fish counter on the North Esk, Dunkley and Shearer (1982) showed increases in the numbers of salmon ascending the weir at times of high flow. Alabaster (1970) and Gee (1980) noted that soon after higher than average flows salmon tend to progress through counting fences and that angling returns increase. Conversely, Hellawell *et al.* (1974) reported that ascending fish tend to utilise lower than average flows; this they attributed to the differing flow characteristics of the River Frome, a chalk aquafer fed river.

There are various problems in attempting to compare the behaviour of migrants with changes in river hydrology; for example, to which part of the spate does the salmon respond is it the rise in water level, the peak discharge or the accompanying fall? If the fish responds to a change in water levels, is it within 24 hours from the peak, or over a longer period? As a river gauging station may be some distance away from the position of a fish, there may be errors in relating the timing of fish movement to the river discharge. Finally, the internal physiology of the fish may change throughout the year, possibly increasing sensitivity to changes in discharge.

At its simplest the salmon's riverine migration divides into three phases, summarised by Milner (1990) as an ascent phase, a quiescent phase and a spawning run. The effects of flow on the behaviour of Spey salmon appear to vary during each stage. During the ascent phase, flow appeared to have little effect on the over-all movements of salmon, though daylight movements during this phase were closely related to increases in discharge. Other studies using fish counters have shown similar trends. Dunkley and Shearer (1982) and Welton *et al.* (1990) found increases in daylight movements of salmon ascending fish counters during spate conditions.

A general analysis of movements with respect to mean daily flows, after the ascent phase was completed, showed that salmon moved at significantly higher flow rates during July 1988, and during June and August 1989. However, by refining the analysis to include only the movements away from a holding pool, ie the stimulus needed for a resting salmon to begin movements, a closer association between movement and elevated flow was found. Thus, it seems likely that after a period of relative inactivity in a holding pool, the stimulus which causes fish to recommence migration is linked with an increase in flow rate.

A direct comparison of salmon movements with the hydrograph (Figs 13a-d) showed that fish began progress at all stages of the spate event, although movements after the peak were the most common. This comparison also indicates that salmon may respond to the spate but that a movement up stream may occur some time later.

These findings agree with those of Clarke and Purvis (1990) for the River Tywi system in Wales. They showed that following the quiescent period nearly all significant movements (>2 km) were initiated during flood events.

Tributary entry in the Spey was also closely associated with increased discharge, and agrees with Webb and Hawkins' (1989) findings for the Girnock Burn.

Several Spey salmon showed behaviour patterns which might be interpreted as indicating homing behaviour associated with increased tributary discharges. For example, F1.88 (which eventually spawned in the River Dulnain) made several up-stream and down-stream movements towards the tributary throughout the summer. It also progressed further up the main stem, beyond the confluence, only to later return down stream, indicating exploratory behaviour. Fish F4.89 and F44.89 showed similar behaviour with respect to the Avon. Some of the excursions towards the tributary began well down stream from the confluence area. Webb (1989, 1990) showed similar behaviour for salmon ascending the tributaries of the Tay.

The behaviour exhibited here may be characteristic of salmon searching for the correct cue to their natal stream. Hasler and Scholz (1983) suggested that salmon orientate towards chemical cues from their home streams, while Nordeng (1977) suggested that pheromones are important. Quinn (1990) reviewed recent findings on salmon migrations and considered whether they are driven by chemical cues or by pheromonal trails.

Although the use of radio telemetry gives a direct method of monitoring salmon movements with respect to flow and other environmental variables, the small numbers of fish released preclude the development of a

relationship for the movements of salmon on the Spey as a whole. Despite this drawback there is evidence to suggest that increases in river discharge play an important part in the up-stream migration of salmon both within the main stem Spey and, in particular, during tributary entrance.

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Finally, I thank my wife Lesley, and many colleagues at the Marine Laboratory including Tony Hawkins, Gordon Smith, Alastair Johnstone, and John Webb of the Atlantic Salmon Trust, for their advice and support throughout the study.

Summary

The results are presented from a radio-tagging study carried out on the River Spey during 1988 and 1989. A total of 46 salmon and 23 grilse was radio tagged and released. Spring salmon, those entering before 1 May, migrated to and subsequently spawned in the upper reaches of the Spey, while summer salmon remained in the lower reaches. This pattern was also found for grilse; those entering during June progressed to the upper reaches, whilst August entrants remained close to their release point.

The riverine migration of the fish fell into four phases firstly an ascent phase, secondly a quiescent period, thirdly a further ascent towards spawning areas, and finally a down-stream migration as a kelt. The distance travelled and the duration of each phase varied throughout the season.

Movements in relation to river discharge were analysed and some associations were found for both tributary entry and daylight movements. In general, most fish migrations were nocturnal.

Anglers on the Spey recaptured 11 radio-tagged fish, one other fish being recaptured on the Findhorn; data on recapture time and vulnerability are presented.

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